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FEEDING ECOLOGY OF LION (*PANTHERA LEO*) IN THE KAROO NATIONAL PARK

By

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DECLARATION

I, Robert Le Brun, declare that the contents of this thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

4th November 2024

Signed

Date

ABSTRACT

Lion, *Panthera leo,* is categorized as Vulnerable by the IUCN and their conservation is a global priority. Lion populations find themselves increasingly confined to small, fenced reserves (< 100 000 ha) and these confined lion populations can aid lion conservation efforts but need careful management. Following the reintroduction of lion into the Karoo National Park (KrNP) in 2010 there have been multiple escapes from the reserve's fenced boundaries. These breakouts required expensive management intervention, lead to human-wildlife conflict, the euthanasia of some lion, and are ultimately bad for lion conservation. Understanding the drivers of lion breakouts is necessary to enable sensible pre-emptive management strategies that will minimize breakouts, reduce human wildlife conflict, protect prey populations, and ensure healthy ecosystem function.

Both social dynamics and nutritional constraints can drive lion dispersal. This study focusses on lion feeding ecology and more specifically the prey species preferred and terrain characteristics of preferred hunting habitat. This project provides a greater understanding of lion feeding ecology in a small arid reserve and is thus of benefit for KrNP and other small wildlife reserves with lion, especially other reserves in semi-arid to arid regions, as well as lion conservation efforts at a global scale.

Recent and historic lion diet in KrNP was analysed using historic field ranger GPS cluster analyses data, and recent GPS cluster data obtained from this study. Lion hunting habitat and the key parameters driving hunting habitat selection are investigated by measuring multiple physical attributes associated with kill sites. For each kill site, identified through GPS cluster analyses, the associated landscape type, vegetative cover, rockiness, visibility and prey availability are estimated on site.

GPS cluster analysis resulted in 144 confirmed kill sites visited and 119 where large prey species (>50Kg) were identified to species level. Kudu (*Tragelaphus strepsiceros*), eland (*Tragelaphus oryx),* red hartebeest (*Alcelaphus buselaphus caama*), and gemsbok (*Oryx gazella),* made up 89% of the large prey consumed. Eland were the most consumed species and contributed the most to the total large prey biomass consumed (40%), double that of kudu which contributed the second most (19%). The 10-year historic GPS cluster data revealed kudu as the most commonly consumed large prey species (27%) and eland the greatest contributor to biomass consumption over the 10 years by lions (30%). The lions also indicated an ability to adapt their diet according to environmental conditions where gemsbok contributed proportionally more to the diet, than in the other years, during the peak of the drought in the Karoo.

An analysis of the preferred hunting habitat of lions on a broad landscape scale showed that lions prefer to feed in the drainage line woodland of the KrNP. This could potentially be attributed to the greater cover within this landscape. The most important fine-scale terrain characteristics in defining kill sites was the vegetative cover and visibility/openness. The terrain rockiness and ruggedness within a 5m radius around the kill site also proved significant.

Lions showed a preference for kudu and eland, and preferred hunting habitat with greater cover. This study indicates that lions are largely dependent, especially in semi-arid areas with uneven distribution of vegetational cover, like the KrNP, on access to optimal hunting habitat where prey are catchable and not necessarily the most abundant. This study does not only provide a greater understanding of lion feeding in Karoo National Park which can assist management with decisions relating to lion management and the reduction of lion breakouts, but also provide much needed data on lion feeding ecology in semi-arid regions.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

APPENDECIES

GLOSSARY

Acronyms

DNA	Deoxyribonucleic acid
Fig.	Figure
GIS	Geographic Information Systems
GPS	Global Positioning System
IUCN	World Conservation Union
Km	Kilometers
Km^2	Kilometers squared
KrNP	Karoo National Park
masl	Metres above sea level
m	Meters
nMDS	Non-metric MultiDimensional Scaling
RBI	Relative Biomass Indices
RHB	Red Haartebeest
SANParks	South African National Parks
SD	Standard Deviation
SE	Standard Error
VHF	Very High Frequency (30-300 MHz; 10-1m)
QGIS	Quantum GIS

CHAPTER 1

GENERAL INTRODUCTION

1.1 Lion status and their ecological importance

The African Lion *(Panthera leo)* functions as a flagship species for terrestrial biodiversity conservation (Loveridge *et al.,* 2009). Apex predators are essential in maintaining the balance and functionality of ecosystems (Mills *et al.,* 1978). A decline in lion numbers may have multiple negative ripple effects on other species, such as the destabilization of herbivore-plant interactions, reduction in scavenger activity, and reduction of diversity (Loveridge *et al.,* 2007; Davies *et al.*, 2016). Lions alter prey behaviour and abundance (Valeix *et al.,* 2009), which resultantly, affects habitat use and overall condition (Gittleman & Harvey, 1982). Lions' iconic stature means that they are a significant tourist attraction and are thus an economic incentive for many reserves (Kerley *et al.,* 2003, Herrmann, 2004). Consequently, the conservation of lions has promoted the protection of multiple large habitats, indirectly benefiting many other less recognized species (Loveridge *et al.,* 2009).

According to the IUCN Red List, the African lion is categorized as Vulnerable (Bauer *et al.,* 2016), with declines experienced throughout Africa (Fig. 1.1), except in the southernmost countries – Namibia, Botswana, Zimbabwe, and South Africa (Bauer *et al.,* 2015). It is believed that, in the next 20–40 years, almost half the unfenced lion populations could decline to near extinction, thus lion conservation is a global priority (Packer *et al.,* 2013).

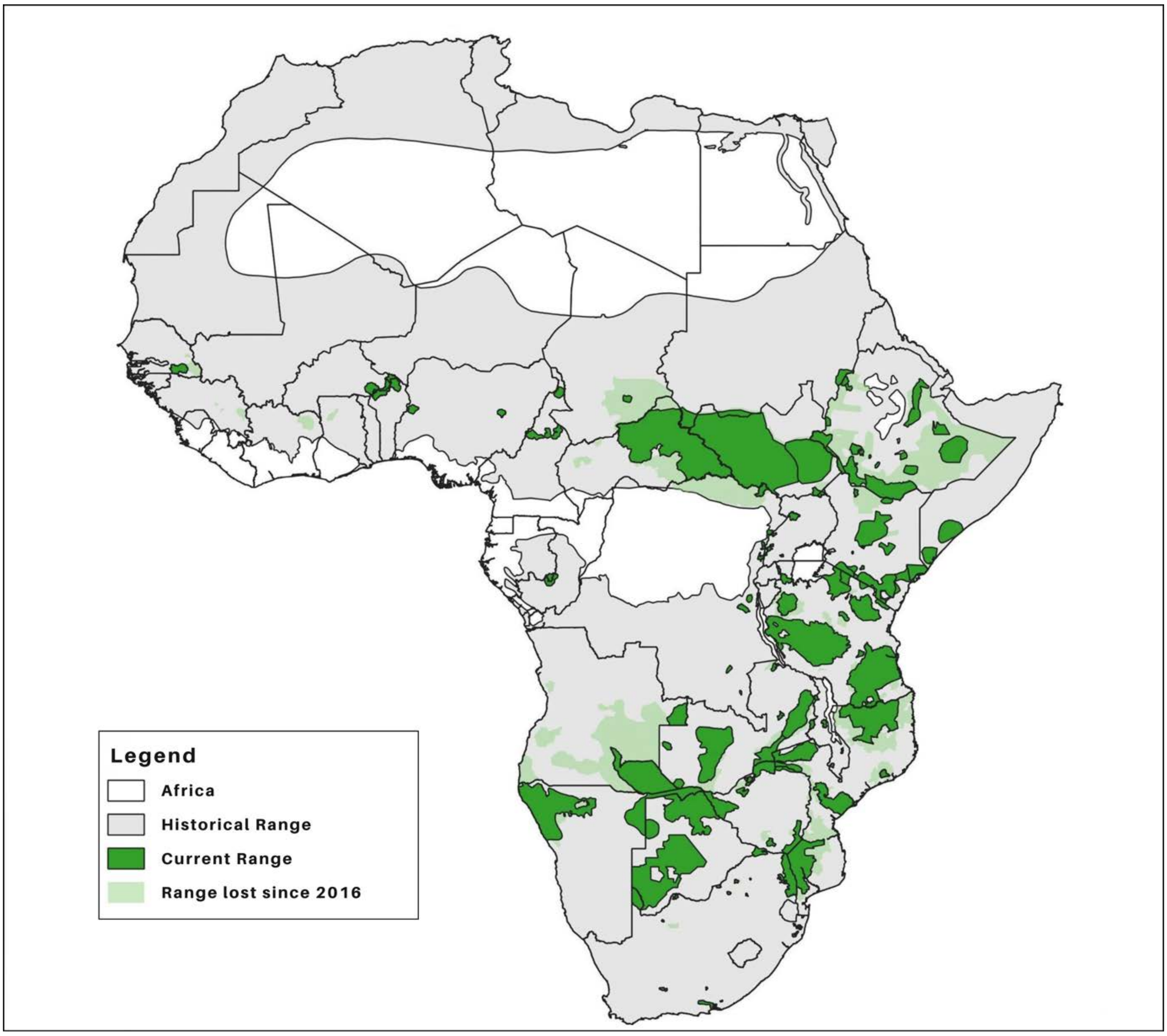

Figure 1.1 Map of the historical (shaded grey) and current (dark green) lion distribution within Africa, and the range lost since 2016 (light green) (Bauer *et al.*, 2018).

Drivers of the decline in lion numbers are generally well understood, although the respective threats' importance varies spatially and temporally (Packer *et al.,* 2013; Lindsey *et al.,* 2017; Bauer *et al.,* 2022). Commercial and subsistence hunting is the most significant direct threat to lions in East and Central Africa, while logging and agriculture that results in habitat restriction, are the most significant indirect threats to protected areas in Central, Eastern, and Western Africa (Tranquilli *et al.,* 2014). More recently, human-lion conflict and prey depletion, largely due to the bushmeat trade, has also been identified as a key determinant in lion declines (Bauer *et al.,* 2022).

In South Africa, most lions were eradicated from their historical range by the 1900s (Nowell & Jackson, 1996), but some populations persisted, with an approximate population of 1 875 individuals remaining as estimated in the early 2000s – with some 1 700 individuals in Kruger National Park (Ferreira & Funston, 2010), 125 individuals in Kgalagadi Transfrontier Park (Castley *et al.,* 2002; Funston, 2011), and fewer than 50 individuals in the Greater Mapungubwe Transfrontier Conservation Area (Fig. 1.2, Miller *et al.,* 2013). Between 1958 and 2018, authorities reintroduced 748 lions into 59 different reserves throughout South Africa (Miller *et al.,* 2013). Some of these reintroductions, in larger reserves such as Hluhluwe-iMfolozi Park (HiP) & Madikwe, have resulted in lion population increases surpassing 50 individuals (Miller *et al.,* 2013). However, most of these reintroduced lion populations are small and enclosed in small fenced areas (< 100 000 ha), which are often isolated (Miller *et al.,* 2013). It is argued, by some, that these small and isolated populations, like that of Karoo National Park (KrNP, 88 307 ha), are of minimal conservation value due to the lack of genetic purity of the populations, the inability to function as stand-alone populations and the inconsistency (and complexity) of stakeholder desires and objectives for the respective populations (Slotow & Hunter, 2009). According to a report by the IUCN in 2006, only the Kruger and Kgalagadi populations were considered 'viable' in South Africa, whilst the Hluhluwe-iMfolozi and Mapungubwe populations were considered 'potentially viable' (Miller *et al.,* 2013).

However, the management of the small lion populations throughout South Africa comply with meta-population functioning and thus do contribute to the conservation of the species (Selier *et al.,* 2024). The meta-population management framework accepts that translocations between reserves and regions, guided by the social dynamics of lions (Ferreira & Hofmeyr, 2014), are the best and an essential method (Miller *et al.,* 2013) to mimic natural dispersal of lion genetics and demographics (Olivier *et al.,* 2009). Resultantly, South Africa's meta-population of around 750 lions is one of the largest lion conservation units in Africa (Ferreira & Hofmeyr, 2014; Selier *et al.,* 2024).

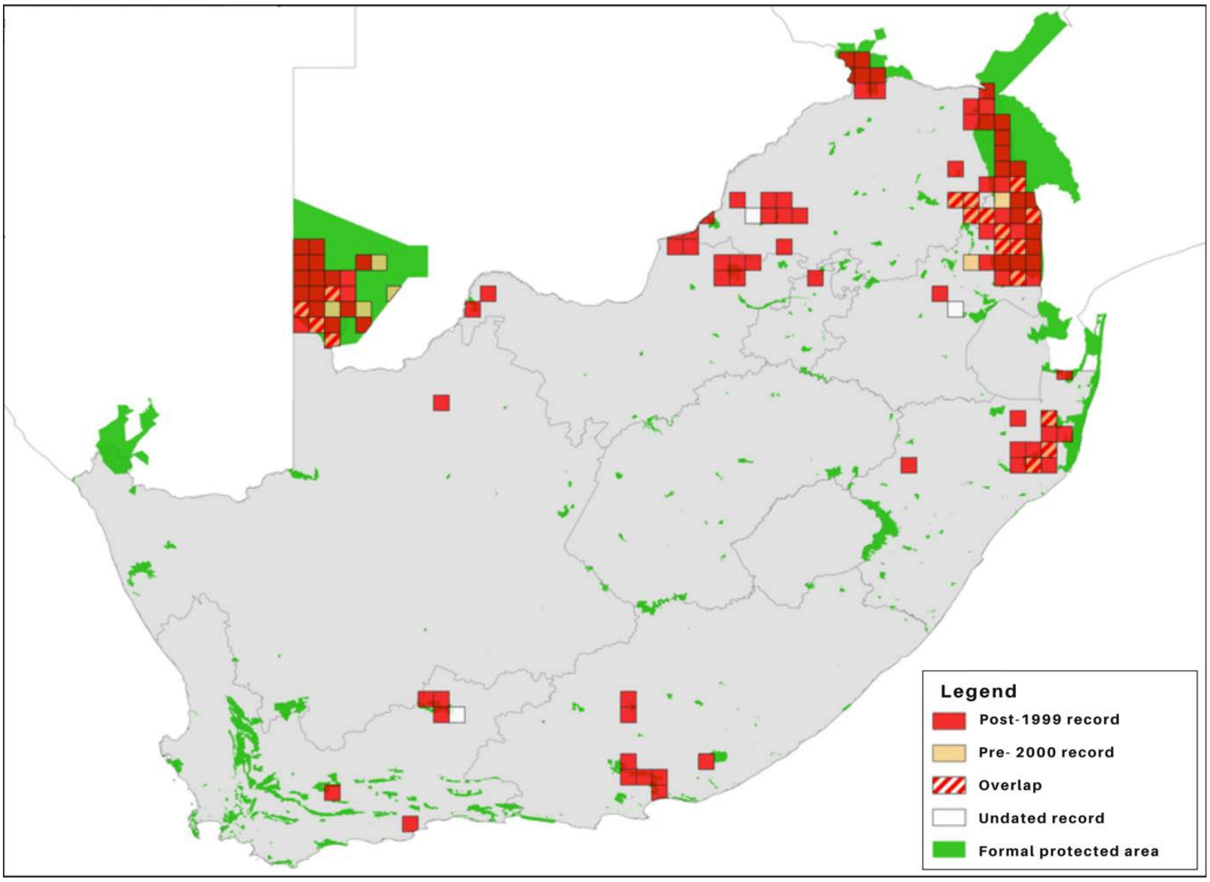

Figure 1.2 Map indicating the distribution records for lions within South Africa – post-1999 only (red), pre-2000 only (orange), post-1999 and pre-2000 records overlapping (diagonal red stripes), undated record (white) and formal protected areas (green) (Miller et al., 2016).

1.2 Lion characteristics

Lions are Africa's largest carnivore weighing, on average, 190 kg for males and 126 kg for females (Skinner & Chimimba, 2005). Lions are the only truly social felid living in prides with between 1 to 9 males and 2 to 18 females (Schaller, 1972; Mosser *et al.* 2009). Generally, the pride is established by related females, and their young (Scheel & Packer, 1991). All pride members contribute in the daily activities of; rearing of cubs (Packer *et al.*, 2001), territory defence (Heinsohn, 1997; Lehmann *et al.,* 2008) and hunting (Stander, 1992a). The likelihood of a successful hunt increases with more individuals, however prides may seperate into "fission-fusion" units if food availability is limited (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992a; Heinsohn & Packer, 1995; Lehmann *et al.,* 2008). Localized variation in the availability of habitat and prey can affect the pride dynamics and behaviour (Patterson, 2007). Lions generally have large home ranges, due to their high metabolic requirements (Gittleman & Harvey, 1982; Loveridge *et al,* 2009). However, these home ranges can vary considerably in extent in reaction to landscape features and resource distribution (Skinner & Chimimba, 2005; Lehmann *et al.,* 2008). Lions defend and define territories by roaring, scent-marking and patrolling the areas while attempting to avoid unsought encounters with other lion prides (Schaller, 1972). Lions are primarily nocturnal, hunting during the night and seeking shade to rest during the heat of the day (Eloff, 1984; Stander, 1992b; Mills *et al.*, 1995; Packer *et al.,* 2011).

1.3 Lion foraging diet and its determination

Food consumption by lions varies based on prey availability, the size of prey, capture success (Green *et al.*, 1984; Hayward *et al.,* 2007) and seasonality (Stander, 1992b). The hunting techniques used and the prey targeted by lions varies according to the pride size, pride dynamics, terrain and vegetation (Stander, 1992b; Davies *et al.*, 2016). The selection of prey by lions can change seasonally and according to environmental fluctuations that, in turn, can affect herbivore aggregations (Carlsson, 2005; Davidson *et al.*, 2013). The hunting behaviour of lions, the influence of environmental variables in determining kill locations, and the significance of these variables across different ecosystems are poorly understood (Davies *et al.*, 2016).

Large carnivores use a lot of energy when hunting (Carbone *et al.*, 1999) and target prey that can provide sufficient energy i.e. more than what is expended during the hunt (Carbone *et al.*, 1999; Radloff & du Toit, 2004). Furthermore, lions target prey parts that provide the greatest energetic profitability (Ruhe *et al.,* 2008). Resultantly, large carnivores usually target larger prey species that weigh 45%, or greater, compares to that of the predator's weight (Carbone *et al.*, 1999; Radloff & du Toit, 2004). That said, lions favour prey that are old, injured, young, pregnant, alone or preoccupied with breeding such as males during the rut (Sinclair & Arcese, 2013; Pereira *et al.*, 2014).

Multiple factors affect a hunt, these factors can be classified according to the prey-, the lion- and the environmental-related factors (Stander & Albon, 1993). Hunting efficiency and probability of hunting success, in open habitats, improves when lions hunt together (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992a), especially when hunting large prey (Schaller, 1972; Scheel & Packer, 1991). Lions can display coordinated hunting cooperation when in prides or two or more individuals (Stander, 1992b). When hunting prey, lions conceal themselves by stalking and ambushing from hidden locations, such as behind grass tufts or dense vegetation (Schaller, 1972; Scheel & Packer, 1991; Davidson *et al.*, 2012; Eby *et al.*, 2013; Loarie *et al.*, 2013; Davies *et al.*, 2016), landscape curvature (Hopcraft *et al.*, 2005) or the cover of darkness (Van Orsdol, 1984; Packer *et al.*, 2011; Preston *et al.*, 2019). Lions generally immobilise their prey by grasping the neck or throat area and suffocating the prey (Schaller, 1972). Other capture techniques have been recorded, in the Kalahari, where lions target and try dislocating, and thus immobilise, inherently weak areas of the body such as the vertebral column at the lumbo-sacral joint (Eloff, 1964).

Lion dietary profiles assist in understanding predator-prey demographics (Owen-Smith & Mills, 2008) and lion population dynamics (Becker *et al.*, 2013), which in turn can assist management decisions relating to lion management. Although lion diet estimates and preferences have been studied comprehensively (Schaller, 1972; Bryden, 1978; Viljoen, 1993; Power, 2002a; Power, 2002b; Hayward & Kerley, 2005; Davidson *et al.*, 2013; Miller *et al.*, 2013) there has been limited research carried out in arid to semi-arid environments (Stander, 1992b; Davidson *et al.*, 2013; Beukes *et al.*, 2017).

Lions show preferences for specific prey species (Rapson & Bernard, 2007; Owen-Smith & Mills, 2008) and prey preference are estimated by identifying the numbers of a specific prey species killed in relation to availability of those species (Hayward & Kerley, 2005; Rapson & Bernard, 2007; Davidson *et al.*, 2013). Power (2002b) estimated that an adult lion consumes between 4.1 - 4.6 kg of meat per day in Madjuma lion reserve in the Limpopo province, which is a similar to estimates from other studies in the Kruger National Park (5.1 kg/lion/day; Bryden, 1978), the Serengeti (5 kg/lion/day; Schaller, 1972) and a dry season study in the Savuti (4.6 kg/lion/day; Viljoen, 1993). Lion prey mass ranges between 0.67 – 1 540 kg (Radloff & du Toit, 2004) but preferred prey mass is estimated to be between 92 – 632 kg (Clements *et al.*, 2014), or around a mean of 350 kg (Hayward & Kerley, 2005). Few potential prey species in KrNP are equal or greater than 350 kg, eland (*Tragelphus oryx*) being the only exception (Skinner & Chimimba, 2005; Spies, 2017). In the arid Kalahari, Beukes *et al.* (2017) found that collectively, gemsbok (*Oryx gazella*), wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus caama*) and eland contributed 92% of the species consumed. Specifically, gemsbok was the most preferred and the most available (abundant and widespread) of the prey species (Beukes *et al.*, 2017). Prey species that are not preferred, but are within the preferred weight range, generally have a morphological adaptation (or a variety thereof) to avoid being preyed upon such as horns that can fend off the predator, occurring in low densities, or by displaying antipredation behaviours like increased vigilance or forming larger herd size (Hayward & Kerley, 2005). Ultimately, the dynamics of large prey were found to be key drivers of lion density, demography and pride dynamics in the Kgalagadi and Hwange National Park (Beukes *et al.*, 2017; Valeix *et al.*, 2009).

Even though prey smaller than 50 kg are generally avoided (Hayward & Kerley, 2005) they serve as “top ups” between larger kills (Eloff, 1984). This small prey intake could increase when lion hunt solo, as hunting success of larger prey generally increases with larger prides (Packer & Pusey, 1997). Additionally, Stander (2003) and Beukes *et al.* (2017) found that a substantial proportion (24% - 32%) of lion diet, in arid environments, comprises of smaller herbivore species including porcupine (*Hystrix africaeaustralis*), springbok (*Antidorcas marsupialis*), common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*). Specifically, springbok was the most selected medium prey in the arid reserves of southern Africa, and accounted for 29.1% of killed prey, in four different locations

(Hayward & Kerley, 2005). However, Beukes *et al.* (2017) found that smaller prey contributes less than 4% to the total biomass consumed by lions.

Male lions, whether hunting solo or in coalitions, generally pursue larger prey like buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*), whilst females primarily prefer medium-sized herbivores like blue wildebeest and plains zebra (*Equus quagg*) and generally display a broader prey selection (Funston et al., 1998; Radloff & du Toit, 2004). It remains uncertain whether lions' prey preferences comes from deliberate selection or the relative ease of capture (Hayward et al., 2011). A review of 32 dietary studies within 42 different lion ranges by Hayward et al. (2007) revealed a significant preference for gemsbok, buffalo, wildebeest, giraffe, and zebra. Among carnivores, lions exhibit the widest range of prey selection and the least dietary overlap with other predators (Hayward & Kerley, 2005). In areas where prey is scarce, such as the arid Kgalagadi Transfrontier Park, greater resource partitioning among carnivores, specialized hunting strategies, and increased dietary flexibility are observed (Mills, 2015).

In the Kalahari there was no significant temporal variation in lion diet seasonally, but there was a marked spatial difference when considering terrain (Beukes *et al.*, 2020). Rainfall, soil nutrients and temperature affect prey biomass which in turn influences lion density (Celesia *et al.,* 2009). In KrNP significant large and fine-scale differences exist between the vegetation, landscape and topographical structure (Spies, 2017) and such large and fine-scale differences create variability in key resources that influence how herbivore and prey species utilize the landscape (Davies *et al.*, 2021; Beukes *et al.*, 2020). Furthermore, lions seek areas that increase prey "catchability" rather than overall prey abundance, such as denser vegetation which typically improves hunting success (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012; Davies *et al.*, 2016). KrNP has 15 dominant plant communities of which the majority are open and sparsely vegetated (Rubin & Palmer, 1996; Bezuidenhout, 2016). It is thus possible that not all of the KrNP landscape can be considered viable lion hunting habitat and that fewer lions can be sustained in this environment than overall prey numbers might suggest. Understanding what lions' prey on and where they kill these prey items, is thus key for the long-term management of the KrNP lion population.

1.4 Methods for determining Lion diet

Various methods have been used to assess lion diets, including stomach content analysis (Smuts, 1979), faecal analysis (Mukherjee et al., 1994; Breuer, 2005; Banerjee et al., 2013; Davidson et al., 2013), spoor tracking (Eloff, 1984), continuous follows (Stander, 1992b), opportunistic observations (Mills, 1984; Rapson & Bernard, 2007; Owen-Smith & Mills, 2008), and global positioning system (GPS) cluster analysis (Pitman et al., 2012; Tambling et al., 2010; Tambling et al., 2011). Additionally, DNA analysis has been used to determine the diets of other predator species, such as wolves (*Canis lupus*) and the leopard cat (*Prionailurus bengalensis*) (Reed et al., 2004; Shehzad, 2011).

Continuous follows are largely considered the most accurate technique used to obtain lion feeding habits (Hayward & Kerley, 2005; Tambling & Belton, 2009), with other techniques not providing definite information on the kill sites or these methods provide some bias towards either smaller or larger prey (Mills *et al.*, 1978; Tambling & Belton, 2009). Continuous observation however is largely unfeasible due to financial or logistical constraints (Beukes, 2016). Opportunistic observations have inherent bias favouring large prey items due to predators spending more time feeding on a larger carcass and, generally, leaving more remains (Mills, 1984).

Spoor tracking as a method to determine carnivore diet is an effective, non-invasive technique, particularly in areas that are challenging to access by vehicle (Eloff, 1984; Bothma & Le Riche, 1984; Mills, 1992; Stander *et al.*, 1997; Melville *et al.*, 2004). Spoor tracking can provide a detailed chronological account of a predator's movements and feeding behaviour (Eloff, 1984; Stander *et al.*, 1997). However, the ease and detail of spoor tracking varies significantly according to substrate (Bauer *et al.*, 2014) and the level of expertise of the tracker (Stander *et al.*, 1997). Accurate spoor tracking and interpretation is reliant on a limited number of individuals with vast experience and a high-level of expertise, and this skill-level is mostly restricted to indigenous communities, like the San people (Stander *et al.*, 1997). Currently, the decline in wilderness knowledge amongst traditional prople, like with the San (Fabricius & de Wet, 2002), has thus lead many researchers and managers to more modern techniques and technologies (Stander *et al.*, 1997).

Scat (faecal) analysis is conducted by identifying any undigested prey remains such as bones, quill, hair and hoof that are found with the collected scat (Ruhe *et al.*, 2008; Tambling *et al.*, 2012). The undigested hairs are further examined microscopically to identify the cuticular scale patterns and cross sections of the medullary structure which are compared against a reference library to confirm species identification (Keogh, 1983; Mukherjee *et al.*, 1994). The method can be effective to identify small prey items, can be used to estimate the mass of prey species consumed (Ruhe *et al.*, 2008) and can provide an indication of the overall diet which make spatial and temporal dietary comparisons possible

(Trites & Joy, 2005). However, the method does not define the age and the sex of the prey, nor does it determine where the prey was scavenged or hunted (Breuer, 2005). Scat analysis also often over represents smaller prey species (Floyd *et al.*, 1978, Beukes *et al.*, 2017).

Collars with Global Positioning System (GPS) technology, fitted to predators, act as data loggers that gather useful information and insights into feeding habits and predator-prey dynamics (Anderson & Lindzey, 2003; Sand *et al.*, 2005; Tambling *et al.*, 2011; Broekhuis *et al.*, 2019). The GPS technology, with its recent advances, is cost effective and allows for locations to be accurately depicted from satellite communications (Merrill *et al.*, 2010). Clustered data points where predators spent a lot of time within a given radius ("GPS clusters") can indicate sites where they were feeding on large prey and is referred to as the GPS cluster method (Merrill *et al.*, 2010; Tambling *et al.*, 2010). GPS clusters are visited by a researcher and the site is investigated to confirm if there are prey remains present (Anderson & Lindzey, 2003). These prey remains, such as bones, jaws, horns, and hair, if present, can allow researchers to estimate the age and sex of the prey and assess its health before death (Sinclair & Duncan, 1972; Blecha & Alldredge, 2015). GPS cluster analysis provides information on the time, location and regularity of kills (Sand *et al.*, 2005) and is especially useful in challenging terrains where traditional approaches like direct observations and scat collection, are largely impractical in determining predator diet (Martins *et al.*, 2011; Fröhlich *et al.*, 2012). Moreover, spatial data from the GPS collars can provide additional insights into landscape usage by the predator, its hunting habits, predator-prey dynamics and indicate potential habitat risk zones for livestock depredation (Merrill *et al.*, 2010; Pitman *et al.*, 2012; Latham *et al.*, 2015; Davies *et al.*, 2016).

The GPS cluster method often provides an exaggeration of large prey items (Tambling *et al.*, 2012), as small prey items are generally consumed too fast to be found using GPS cluster analysis (Bacon *et al.*, 2011; Tambling *et al.*, 2012). Additional challenges with the GPS cluster method include, the obstruction of the collar signal to the satellite which provides errors in GPS location accuracy, GPS device malfunctions, limited battery life capacity of the GPS collar and the complexities associated with the capturing of animals and ethics to applying or removing collars (Boitani & Fuller, 2000; Frair *et al.*, 2010; Hebblewhite & Haydon, 2010). Technological advancements are fast addressing shortfalls in GPS cluster analysis for biological studies, thus creating new opportunities for further insight into animal ecology (Tomkiewicz *et al.*, 2010; Kays *et al.*, 2015; Pimm *et al.*, 2015).

The various methods that exist to evaluate the diet of predators each have their own logistical and financial constraints and inherent biases. However, to successfully conserve large carnivores, especially within small reserves, it remains essential to gain an understanding of their feeding habits and behaviour (Tambling *et al.*, 2012). In KrNP GPS cluster analysis provides the most feasible way to study lion diet as the mountainous terrain renders continuous follows and direct observations unfeasible (Martins *et al.*, 2011; Fröhlich *et al.*, 2012). The inaccessible terrain and limited road network also make the discovery and collection of lion scat samples in sufficient numbers across the area inviable without the help of specific location data.

The research proposed here will investigate the recent and historic prey use of lions in the KrNP. The study will also identify the broader landscapes preferred by lions for hunting and investigate which fine-scale habitat features are characteristic of lion kill sites. This information will aid management authorities with the management of lion within KrNP. A combination of methods including historic and recent GPS cluster analysis will be used to identify lion diet, while lion kill site locations as determined from GPS cluster analysis will be assessed to identify and characterise lion feeding habitat.

1.5 Lion hunting

Understanding predator space-use, and the scale thereof, is essential when managing diverse wildlife systems where lions can significantly influence the entire ecosystem and the associated ecological processes (Boyce, 2006; Ciarniello *et al.*, 2007; Tarugara *et al.*, 2024). Semi-arid landscapes, like KrNP, are typically heterogeneous (Tongway & Ludwig, 2005) as species space-use is driven by the distribution of available resources (Tarugara *et al.*, 2024). The selection of hunting habitat by predators is generally governed by the abundance of prey in a particular habitat or by the catchability of the prey in a certain habitat (Hopcraft *et al.*, 2005). Research has found support for both arguments. In some cases, carnivores select habitats with attributes that increase likelihood of hunting success and thus, select habitat attributes that increase the susceptibility of prey to predation (Hebblewhite *et al.*, 2005; Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Smith *et al.*, 2020). Conversely, multiple studies have shown that carnivores display a preference for habitats with greater prey abundance, with the landscape not significantly influencing the 'catchability' of prey, and predators simply preyed in regions where prey was more abundant (Murray *et al.*, 1994; Pike *et al.*, 1999; Palomares *et al.*, 2001; Spong, 2002).

Furthermore, lion habitat use is largely influenced by prey abundance and proximity to water (Davidson *et al.*, 2012; Sargent *et al.*, 2022; Tarugara *et al.*, 2024). In dry landscapes especially, the availability of surface water largely influences the distribution of herbivores (Sargent *et al.,* 2022). Herbivores tend to aggregate around scarce water sources (Thrash *et al.*, 1995), and for most herbivores, habitat selection is largely influenced by distance to water (Mosser *et al.*, 2009; Valeix *et al.*, 2009; Davidson *et al.*, 2012; Sargent *et al.,* 2022). Lions, thus, have a greater chance of encountering prey near water sources (Valeix *et al.*, 2010). Additionally, multiple studies have displayed that vegetation cover is the driving factor of hunting habitat preference (Van Orsdol, 1984;

Spong, 2002; Hebblewhite *et al.*, 2005; Hopcraft *et al.*, 2005; Riginos & Grace, 2008; Davidson *et al.*, 2012; Tambling *et al.*, 2012; Davies *et al.*, 2016; Loarie *et al.*, 2013). Lions indicate a preference of more open habitats, such as grassland and open shrubland (Cristescu *et al.*, 2013, Courbin *et al.,* 2016), likely because there is a greater abundance of their preferred prey species supported in these habitats (Spong, 2002; Miller *et al.*, 2018). However, when hunting, lions may choose habitats with increased vegetation cover (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012; Elliot *et al.*, 2014). Ultimately, a combination of open and closed habitats are lions preferred hunting habitats (Davidson *et al.*, 2012; Smith *et al.,* 2020 Sargent *et al.*, 2022). Dense vegetation is generally not favoured (Loarie *et al.*, 2013; Smith *et al.*, 2020. However, male lion appears to favour ambush hunting techniques (Loarie *et al.*, 2013) and hence utilize these denser areas more, whereas females who favour cooperative hunting techniques (Funston *et al.*, 1998; Owen-Smith & Mills, 2008) tend to favour less dense areas (Loarie *et al.*, 2013). In the Serengeti, lions also preferred areas with fine scale topographical change alongside riverbanks which provide some cover (Hopcraft *et al.*, 2005; Kittle *et al.*, 2016). Furthermore, fine scale underfoot conditions can potentially also influence hunting habitat preference (Wheatley *et al.*, 2021).

However, studies have recorded successful kills in both open and closed environments indicating that lions display significant habitat flexibility and can adapt their habitat use to improve their own security without reducing hunting success (Sargent *et al.*, 2022; Tarugara *et al.*, 2024).

1.6 Lion dynamics in small reserves

Managing lion populations, or the re-introduction thereof, in small reserves is complex (Miller *et al.*, 2013; Le Roux *et al.*, 2019) as lions are highly vulnerable to anthropogenic factors (Herrmann 2004) and environmental fluctuations (Bauer *et al.*, 2005). This is due to the relative low population sizes of lions, the isolation of these small reserves, and for certain populations like that of KrNP, the arid and resource-poor environment into which the re-introductions occur (Mills *et al.*, 1978; Castley *et al.*, 2002). Three further major challenges in managing small lion populations are: a) a lack of natural/ecological regulation (population control), b) genetic degradation through inbreeding, and c) increased susceptibility to catastrophic events like disease (Miller *et al.*, 2013).

In larger reserves, that are less affected by disturbance, lion populations are often self-regulating, yet in smaller reserves they often overpopulate rapidly and require regular intervention (Miller *et al.*, 2013). The sociality of lions provides some insight into the breakdown of natural/ecological regulatory mechanisms (Miller *et al.*, 2013). Lionesses form prides for two main reasons: to defend their cubs against roaming males, and to defend themselves against other female groups (Packer *et al.*, 1988; Mosser & Packer, 2009). Defence of cubs and territories can be violent and sometimes results in death for members of the pride, including cubs, subadults and even adults (Mosser & Packer, 2009). In most small reserves there are typically few large nomadic males, few rival prides and the pride numbers are relatively small (Druce *et al.*, 2004; Lehmann *et al.*, 2008). These factors enable male lions to hold territories for longer, which limits infanticide (Bygott *et al.*, 1979; Funston *et al.* 1998, Funston *et al.,* 2003; Miller & Funston 2014). As a result, approximately 87% of cubs survive in small reserves (Druce *et al.*, 2004; Kilian, 2003; Lehmann *et al.*, 2008; Miller & Funston, 2014), as opposed to between 40% and 59% in larger reserves (Eloff, 1980; Lehmann *et al.*, 2008; Funston *et al.*, 2003; Funston, 2011). Furthermore, these cubs in small reserves have limited dispersal opportunities when reaching sub-adulthood at an age of two to four years (Miller *et al.*, 2013). Consequently, few of the natural processes that drive cub mortality or sub-adult dispersal occur in small reserves, resulting in the high observed population growth rates (Miller *et al.*, 2013).

Due to the absence of natural population regulatory mechanisms, the populations of lion in small, fenced reserves are generally closer to or above their estimated carrying capacities than in unfenced populations or in populations occurring in larger reserves (Packer *et al.*, 2013). The unnaturally high lion numbers can constrain prey population numbers (Power, 2002a; Tambling & du Toit, 2005), leading to lions searching for prey outside the fenced reserves once prey numbers reach levels where they become unavailable or too difficult to catch. It is also not only absolute prey numbers that are of importance, but also the spatial distribution of potential prey, as not all areas are equally good for hunting (Hopcraft *et al.*, 2005; de Boer *et al.*, 2010; Hayward *et al.*, 2011; Davies *et al.*, 2016). The proportional dietary contributions of prey to lions across varied terrain and habitats can also provide critical information of how lions affect localized ecosystem dynamics through the predation pressures upon their preferred prey species (Le Roux *et al.*, 2019; Beukes *et al.*, 2020).

1.7 Lions in the Karoo National Park

The objective for the KrNP is "to conserve a representative portion of the Nama Karoo ecosystem and its biodiversity, to preserve the ecological integrity of the area, and to provide a natural area for people to enjoy" (Van Heerden, 1993). The previous management plan for Karoo NP of 2008 stated: "To restore and conserve Karoo NP's cultural, landscape and ecological processes, thereby delivering high quality nature-based tourism derived from the Karoo's sense of place and providing benefits to the communities of the Central Karoo district." More recently, the reserves management plan states the reserves' role as: "To ensure KrNP is a key driver of sustainability in the region, by restoring and conserving processes that maintain representative cultural, landscape and biodiversity assets, which facilitate equitable opportunities for the well-being of society and deliver high quality nature- based tourism derived from the Nama-Karoo's sense of place".

Lions were reintroduced into KrNP (Fig. 2.1), in 2010, to reclaim their ecological role as large apex predators and restore natural predator-prey dynamics (Spies, 2017). The reintroduction of lions also re-established the opportunity for scavenging by mesocarnivores within the ecosystem (Ferreira *et al.*, 2011; Codron *et al.*, 2018) and enhance the tourism experience, which further promotes the reserve's preservation (Maciejewski & Kerley, 2013; Spies, 2017).

However, since the lion reintroduction multiple lions have escaped from the reserve's fenced boundaries, some of which travelled over 300 km and took 22 days to recapture, increasing the human-wildlife conflict with the livestock farming communities and stakeholders bordering the park (Ferreira *et al.*, 2011; Spies 2017).

A greater understanding of lion hunting habitat, population dynamics and spatial patterns, within KrNP and other small reserves, are necessary to minimise breakouts, reduce resulting human-wildlife conflict, protect prey populations and, ultimately, ensure sustainable ecosystem performance. This study will provide a greater understanding of lion feeding ecology within the KrNP, that will not only benefit the KrNP itself, but also, small wildlife reserves with lion in general and lion conservation efforts globally. Ultimately for the KrNP, the knowledge acquired from this study will also allow the management to align closer with the KrNP Management Plan (2017) that states "SANParks wishes to restore and maintain the ecological role of large carnivores as apex predators in the terrestrial ecosystem".

1.8 Statement of research problem

Successful management of lions in small, fenced reserves is challenging due to rapid lion population growth, their resultant pressure on prey populations and human-wildlife conflict due to lion escapes from the safety of the protected areas. The KrNP, has experienced these challenges recently with multiple lion breakouts that resulted in high levels of human wildlife conflict and ultimately the culling of multiple lions. This research has thus been initiated in direct response to these consistent breakouts as management need detailed information on lion feeding ecology. A better understanding of whether the availability of sought after prey and preferred hunting habitat are potentially driving lion breakouts is needed for the safeguarding the lions of this reserve.

1.9 Objectives

- To estimate the recent large prey use of lions within the KrNP using GPS cluster analyses.
- To establish whether lion's large prey preference within KrNP has changed over the 10 years since lion re-introduction using historic kill and game census records.
- To determine whether lion select certain landscapes within KrNP more than others for killing large prey.
- To determine whether lions within KrNP show preference for certain fine scale habitat characteristics in pursuit of large prey.

1.10 Structure of the thesis

The thesis comprises five chapters. Chapters 3 and 4 are independent, stand-alone manuscripts to support publication in peer-reviewed journals.

- **Chapter 2** contextualises the KrNP and study site and focuses on the locality, climate, topography, geology and soils, hydrology and artificial water points, vegetation, landscape types, fauna, infrastructure, surrounding land use and human impact.
- **Chapter 3** investigates the recent and historic diet of lion in the KrNP, using kill data obtained from GPS cluster analysis. The comprehensive lion diet information ascertained during this study is compared to historic kill records sourced from the reports of rangers that used a similar approach to obtain some lion diet information since 2010.
- **Chapter 4** assesses kill site locations at both the landscape and local scale level. Kill site locations are evaluated across four broader landscape types (considering slope, vegetation, and altitude), and, at a finer scale, kill site characteristics (visibility, vegetative cover, terrain rockiness, prey abundance) are compared against that of non-kill/control sites.
- **Chapter 5** is a synthesis chapter that aims to relate the most important findings to lion management recommendations within KrNP and identifies aspects in need of further research.

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CHAPTER 2

STUDY AREA

2.1 Introduction

The Karoo National Park (KrNP) is located in the Western Cape province of South Africa (Fig. 2.1). KrNP was officially proclaimed in 1979 when a 72 km^2 piece of communal land was donated by Beaufort West's Town council (Spies, 2017; Saayman *et al.*, 2009). Prior to the donated land forming the core of the KrNP, the portion was a small-livestock farm (Rubin & Palmer, 1996). The KrNP increased in size to 271 km^2 in the late 1980's (Martin *et al.*, 1988) and then onto the parks current size of 883 km^2 (Dippenaar-Schoeman *et al.*, 1999; Saayman *et al.*, 2009; Spies, 2017).

The KrNP forms part of the Great Karoo, South Africa's largest ecosystem that covers approximately 400 000 km^2 (Dean *et al.*, 1995) and 35% of the country's surface area (Bezuidenhout, 2016; Spies, 2017). The KrNP was specifically established to conserve a representative portion of the semi-arid Nama-Karoo biome (Bezuidenhout, 2016; Saayman *et al.*, 2009; Spies, 2017). The KrNP conserves 30% of the recognized endemics of the Nama-Karoo biome (Rubin *et al.*, 2001). Additionally, since the rest camp opening in 1989 (Spies, 2017), the reserve has focused on providing a tourism facility for people to enjoy this natural area (Bezuidenhout, 2016; Ferreira *et al.*, 2011).

Lions were re-introduced into KrNP in 2010 to restore their ecological role as large carnivore apex predators (Spies, 2017).

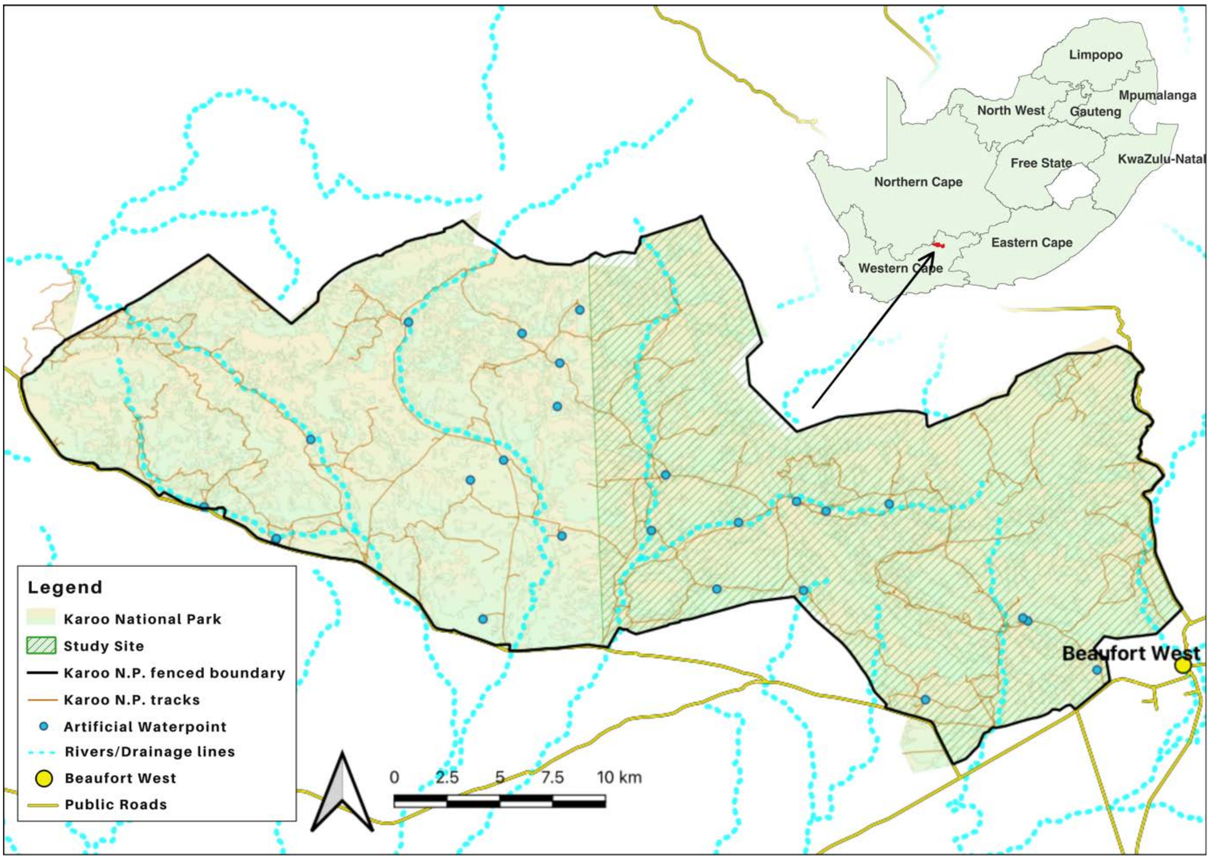

Figure 2.1 Map of the Karoo National Park, and its locality within the greater South Africa (inset). Also shown are the boundary fence, the study site area (hatched green area in the eastern portion of the reserve), prominent drainage lines, the artificial waterpoints, the park's roads/tracks, the nearest town -Beaufort west, and the surrounding public roads (QGIS Development Team, 2021).

2.2 Locality

The KrNP is situated 3 km northwest of Beaufort West in the Western Cape province but on the border with the Northern Cape province of South Africa and is located between 32°10'S - 32°23'S and 22°15'E - 22°35'E. The study was restricted to the eastern half of the KrNP, due to logistical and financial constraints. The eastern part of the park supported the highest lion density at the time and have good representation of all the different landscape types making it possible to achieve the stated objectives. The KrNP is underlain largely by the Karoo Supergroup from the Permian age, which is made up of the Dwyka formation, Ecca group and the Beautfort group (Johnson *et al.*, 2006; Spies, 2017) and is a critical contributor to the 1.6% of the Nama-Karoo biome that is formally conserved (Hoffman *et al.*, 2018). In the more recent years, a shift towards sustainability and community upliftment of the Central Karoo district has been seen (Saayman *et al.*, 2009), largely aided by the increase in tourism throughout the Great Karoo (Saayman *et al.*, 2009; Atkinson, 2016).

2.3 Climate

2.3.1 Historic

The mean rainfall varies from 175 mm - 406 mm annually across the KrNP, with the majority (60% – 75%) falling in summer (Spies, 2017). There is a large variation of rainfall between years (Fig. 2.2) and the coefficient of variation in annual rainfall, decreases from west to east. The KrNP has hot summers (average maximum summer temperature is >32 °C) and cold winters (average minimum winter temperature is 3.5 °C - Spies, 2017). The Great Escarpment mountains, that traverse across the entire reserve and make up a significant portion of the eastern section of the reserve (Spies, 2017). A cool steppe climate prevails at higher elevations, with steep elevation and a precipitation gradient rapidly transitioning to a warm steppe climate in the eastern, southern and western lower lying regions of the KrNP (Spies, 2017). In the winters, mild to heavy frost occurs and snow periodically falls at higher elevations on the Nuweveld Mountains (Spies, 2017). The vegetation growth season generally lasts seven to eight months and is diminished by the cold winter snaps (Spies, 2017). The westerly and north westerly winds, which have a scorching effect on the soil and vegetation, are common throughout the region (Spies, 2017).

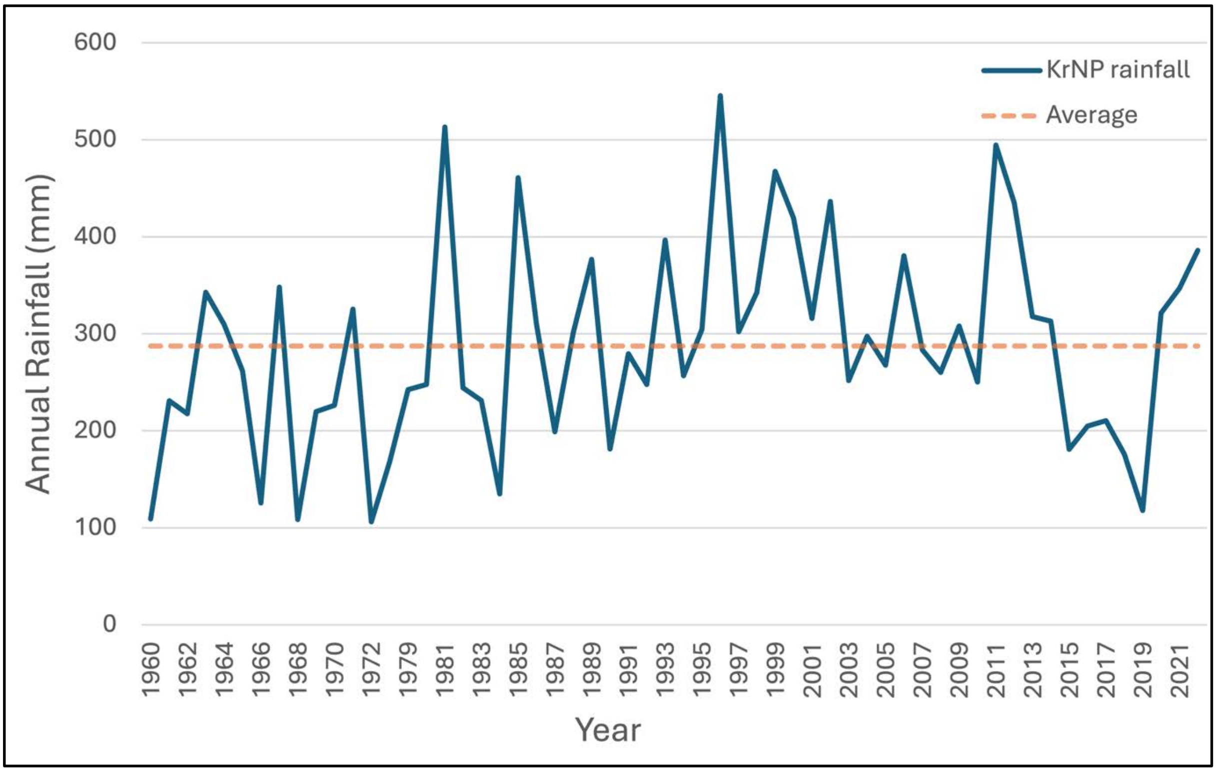

Figure 2.2 The annual rainfall (blue line) and the average rainfall (orange dashed line) recorded by the Agricultural Research Council at Stolshoek, the main camp in the Karoo National Park, from 1960 – 2022 (Moeletsi et al., 2022).

2.3.2 Future

Seventy three percent of Africa's dryland habitats, like the Karoo, are affected by climate change (Hoffman, 2009), resulting in desertification (Meadows & Hoffman, 2007). This trend is expected to continue increasing during the twenty-first century (Schlaepfer *et al.*, 2017; Hoffman *et al.*, 2018). However, certain studies have argued against the expanding Karoo (desertification) hypothesis and found that the carrying capacity has not decreased (Hoffman *et al.*, 1995; Hoffman, 2009; Hoffman *et al.*, 2018).

South Africa's national parks have over the past five to ten decades displayed significant temperature increases and reduced rainfall in most of the parks (van Wilgen *et al.*, 2016). The observed temperatures changes over the last 20–50 year period have, in multiple instances, already reached those predicted near future temperature models (2035), indicating that predicted trends are conservative (van Wilgen *et al.*, 2016). By 2050, the average temperatures within the KrNP are estimated to be between 1.5 °C and 2.5 °C higher (DEA, 2013; Driver *et al.*, 2012; Spies, 2017). This expected change is significant, especially so for the number of days with extreme temperatures where it is predicted that between 16 and 31 more days in the year will reach temperatures exceeding 35 °C (Spies, 2017). Hot extremes, especially if they extend for multiple days, have negative impacts on the fauna and vegetation (Spies, 2017). Rainfall is predicted, in the intermediate and driest scenarios, to be between 20 mm and 80 mm less annually (DEA, 2013; Driver *et al.*, 2012; Spies, 2017), which could result in the rainfall of the region being halved. An increase of 54 mm rainfall annually is the wettest scenario prediction (Spies, 2017). As shown, there is significant uncertainty in the future conditions but under all the possible 2050 scenarios it is predicted that the climatic conditions would remain within the Nama Karoo range experienced currently, making the KrNP a critical area for Nama Karoo conservation (Spies, 2017). Furthermore, the KrNP should aid in climate change mitigation and contribute to a more sustainable future (Spies, 2017).

2.4 Topography

The KrNP can be partitioned into five physiographic units (Dippenaar-Schoeman *et al.*, 1999; Van der Merwe *et al.*, 2015; Spies, 2017), and according to Spies (2017) these are:

- the Southern and Central plains below 1,000 masl
- the South Eastern plains below 1,000 masl
- the Middle Plateau between 1,100 – 1,200 masl
- the Northern Upper Plateau 1,600 – 1,900 masl
- the flat topped Korannasfontein Mountain in the west 1,400 – 1,550 masl

The most significant topographic feature, with the largest area, of the park is the lowland plains south of the Nuweveld escarpment (Fig. 2.3, Spies, 2017). The lower lying plains are interspersed with characteristic Karoo koppies and intersects the largely ephemeral karoo riverbeds (Spies, 2017). These riverbeds within KrNP largely flow to the south through deep gorges in the mountainous areas becoming more gradual sandy riverbeds lower down (Spies, 2017). The Nuweveld escarpment edge is lined with multiple large cliffs, forming the steepest profile (1:100 m) in the KrNP (Spies, 2017). The escarpment and its associated steep south-facing slopes run along the length of the KrNP, but it is most prominent in the east, separating the higher elevated regions in the north and the lower plains in the south (Spies, 2017).

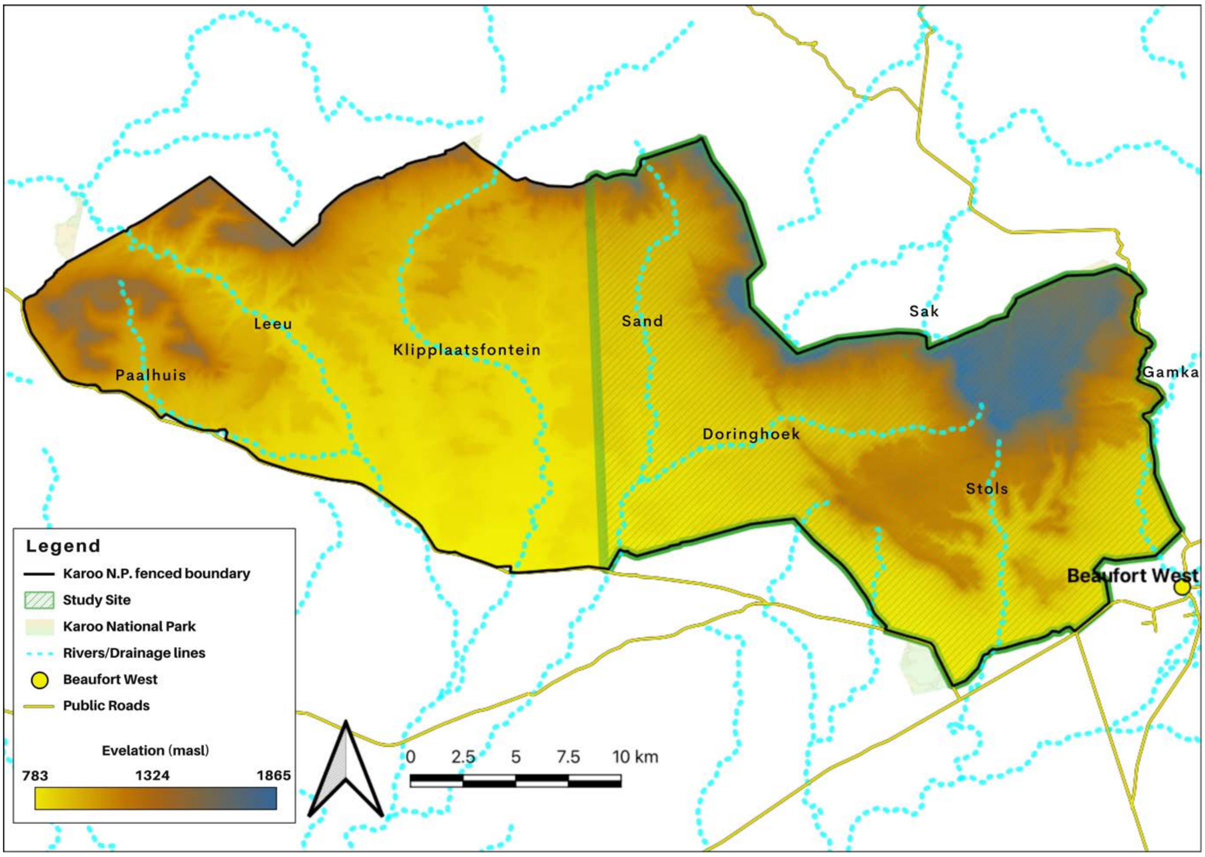

Figure 2.3 Elevation map of the Karoo National Park clearly indicating the higher lying areas (escarpment) in the north and especially north-eastern regions. The study area (hatched green area in the eastern portion of the reserve) and the main drainage lines are also shown with their names (QGIS Development Team, 2021).

2.5 Geology and soils

The KrNP is made up of the Karoo Supergroup from the Permian age, which consists of the Dwyka Formation, Ecca Group and Beaufort Group (Spies, 2017). The Beaufort Group is found above the Ecca Group and contains alternating mudstones and sandstone (Spies, 2017). The younger, Jurassic-age, dolerite dykes and sheets intrude the Beaufort Group, causing metamorphosis and resulting in hornfells and quartzitic rocks (Spies, 2017). Newer Quaternary age deposits, where the majority of the Drainage Line Woodland is found consist of calcrete, alluvium, river terrace gravel and debris (Rubin & Palmer, 1996).

Rock weathering is the prominent soil-forming process, which leads to the formation of orthic topsoil horizons largely related to the Nuweveld Mountain (Spies, 2017). The B-horizons throughout the KrNP are largely dominated by the Glenrosa and Mispah soil forms that are typical of large rocky outcrop areas. The soil is largely 0.05 m – 0.3 m in depth which contains a clay content of between 15 % and 35 % (Spies, 2017). However, the Upper Plateau of the Nuweveld Mountain, in the north-eastern corner of the KrNP, is dominated by the more fertile Oakleaf and Valsrivier soil forms, with a high clay content, of between 20 % and 55 %, and a depth of between 0.1 m - 0.3 m (Spies, 2017).

2.6 Hydrology and artificial water points

The Nuweveld Escarpment forms the watershed between the Central Karoo and Upper Karoo (Spies, 2017). The majority of the KrNP is located south of the escarpment where the water drains southward via various drainage lines. Consequently, multiple smaller rivers sources are high up in the park, such as the Sand, Doringhoek and Stols Rivers that drain into the larger, and important, Sak, Leeu and Gamka Rivers (Fig. 2.3, Spies, 2017). The Leeu River enters the park from the Northern Cape at Brandewynsgat to the west of the KrNP, and flows easterly through the park. The Paalhuis River, Klipplaatsfontein River, Boesmanskop River, Doringhoek River and Sand River, all of which have their catchments on the Nuweveld escarpment within the park, flow southerly into the Leeu River. In the north-east, the Gamka River partially shares its source with the park before it flows in a southerly direction through the park and then out the park (Spies, 2017). The Stolshoek River's source is in the Eastern portion of the KrNP, above the rest camp, where it subsequently it joins the Gamka River downstream. Also, in the north-east, at higher altitude, the Puttersvlei area drains gently towards the north and forms the source of the Sak River (Spies, 2017). The streams and rivers are ephemeral – seasonal, short-lived and dependent on precipitation, largely falling in the winter, to flow. However, some of the large rivers such as the Klipplaatsfontein, Leeu, Gamka, Doringhoek Rivers, can retain flow for extended periods after rain, and water in river pools for even longer (Spies, 2017).

There are multiple small springs throughout the park (Spies, 2017; personal observation). The spring at Kookfontein, in the central section of the KrNP, is the strongest and was historically used for irrigation (Spies, 2017). Ground water is abundant but is not accurately quantified throughout the KrNP. More than 60 boreholes exist which are currently or was historically equipped with windmills, some of which, like in the Doringhoek and Stolshoek areas, extract more than 40 000 litres per hour (Spies, 2017). Some wetlands occur and are mostly found along the large rivers and around the strong springs (Spies, 2017). The northern Upper Plateau and associated mountain slopes generally contain more moisture compared to the southern lower lying plains (Spies, 2017).

2.7 Vegetation

The KrNP falls within two Biomes namely Nama-Karoo, which forms the largest portion of the park, and the Grassland Biome, covering a relatively small section of the park atop the Nuweveld Mountain range (Bezuidenhout, 2016; Spies, 2017).

Within KrNP, a total of 864 plant species, from 355 genera and 93 families have been documented within KrNP (Rubin *et al.*, 2001). Of these 864 species, 121 species (14%) are endemic to the Nama-Karoo, and resultantly KrNP conserves 30% of the known endemics of the Nama-Karoo Biome (Rubin *et al.*, 2001).

The Nama-Karoo biome representation within the KrNP, is made up of the Upper-Karoo bioregion unit and the Lower-Karoo bioregion unit (Bezuidenhout, 2016). The Upper-Karoo bioregion unit is comprised of the Western Upper Karoo, Upper Karoo Hardeveld and the Eastern Upper Karoo vegetation types (Mucina & Rutherford, 2006). The Lower-Karoo bioregion unit is represented by the Gamka Karoo vegetation type (Mucina & Rutherford, 2006). The Grassland biome part of the park comprise of the Karoo Escarpment Grassland vegetation type, and is part of the Dry Highveld Grassland bioregion (Mucina & Rutherford, 2006). According to Bezuidenhout (2016) a third biome is present namely, Azonal Saline vegetation, which is made up of the Inland Saline vegetation unit and is further broken down and represented by the Bushmanland Vloere (AZi5) and Southern Karoo Riviere (AZi6). The vegetation delineation, and their descriptions, is taken from Bezuidenhout (2016) as follows:

A phytosociological study conducted by Rubin & Palmer (1996) described fifteen dominant plant communities in the original 330 km^2 park (mostly the eastern third of the current reserve). The steep elevation and slopes, and the associated precipitation gradients within the KrNP have a significant influence on the diversity of habitat-cum-vegetation units. The high montane grassland plant communities, receive relatively high rainfall and are thus dominated by *Merxmuellera disticha*, *Cymbopogon pospischilii* and *Themeda triandra.* The grass species and Fynbos associated taller forbs such as *Elytropappus rhinocerotis*, *Euryops annae* and *Passerina montane* and sparse, but common, woody plant species like the tree *Sterboom Cliffortia* arborea and the dwarf shrub *Diospyros austro-africana.*

Moving away from the steep escarpment edge, in a south westerly direction, comes with a significant increasing aridity, and the Montane Karoo dwarf shrublands supersede these mesic plant communities with plant species such as *Eriocephalus ericoides, Rosenia oppositifolia* and *Pteronia tricephala* that dominate this unit. In the lower lying valleys and plains, the rainfall is limited and erratic. In these lower regions, the various drainage lines obtain the only woodland plant communities in the park, with the tree *Vachellia karroo,* dwarf shrub *Lycium cinereum*, grass species *Stipagrostis namaquensis* and *Cenchrus ciliaris* being the more predominant species. Bordering these lowland drainage lines are dry forbland plant communities, which are largely dominated by the grass species *Stipagrostis obtusa, Stipagrostis ciliata* and the herbaceous *Pentzia incana*, *Hermannia* species, *Aptosimum* species and *Eriocephalus* species.

The delineation, definition and mapping of the plant communities, together with their related abiotic features, within the KrNP has been well documented but the various studies have yielded mildly different broad and fine-scale results with: Rubin & Palmer (1996) identifying 15 different plant communities, Bezuidenhout & Holness (2005) identifying 7 different broad plant communities, Mucina & Rutherford (2006) identifying 7 different broad plant communities and two biomes and, more recently and used in this research, Bezuidenhout (2016) identifying 15 different plant communities (Fig. 2.4, largely similar to Rubin & Palmer, 1996) and three major ecosystems.

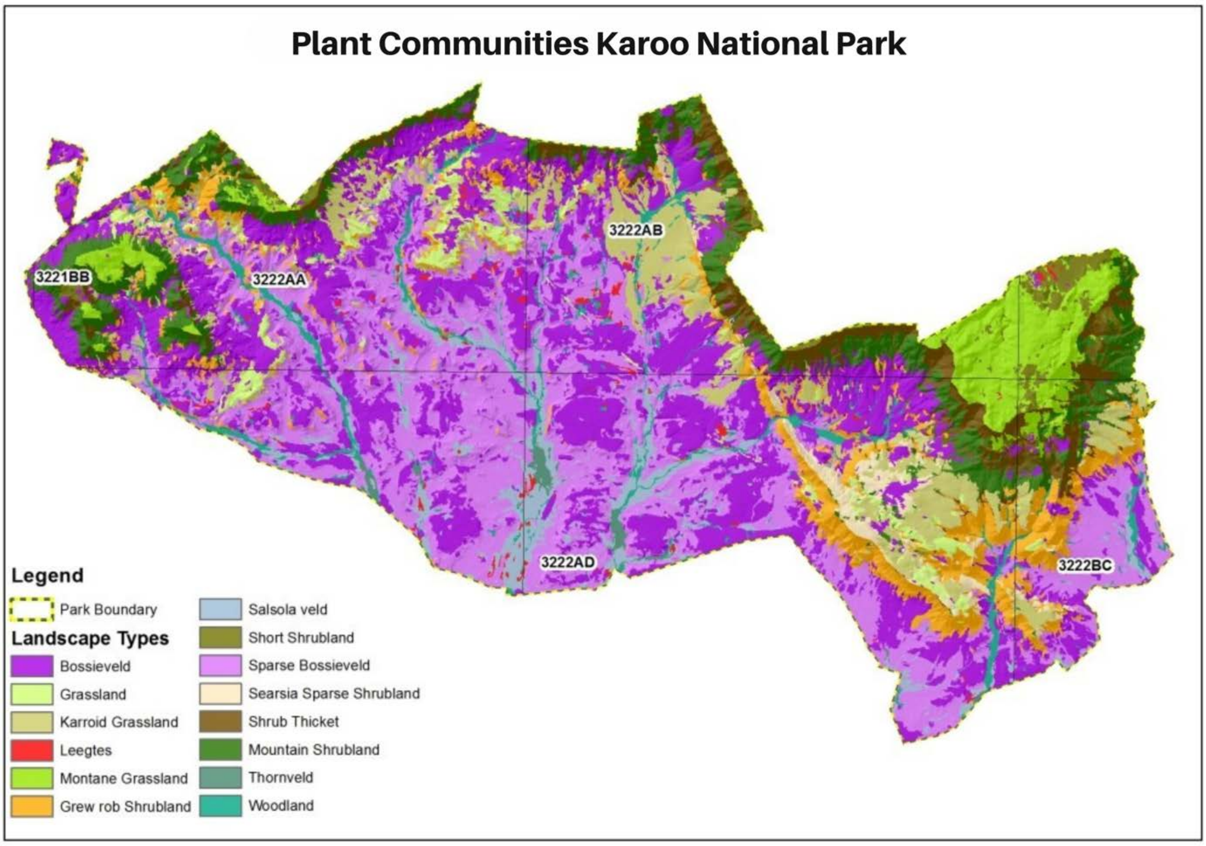

Figure 2.4 Map of the Karoo National Park showing the delineation of the 15 different plant communities also referred to as landscape units by Bezuidenhout *et al.*, (2016).

2.8 Landscape types

For this research, the reserve was divided into four broad landscape types using Bezuidenhout's (2016), three major ecosystems (Nuweveld Mountain plateau and ridges, Terraces of the Nuweveld Mountain midslopes and mid-plateau, and the Valley bottomland with associated drainage lines). The valley bottomland and associated drainage lines were split into drainage woodland (referred to in this study as Drainage Line Woodland) and valley bottomland units (referred to in this study as the Lower Plateau). The landscape units were identified and described as follows by Bezuidenhout's (2016):

"1. Nuweveld Mountain plateau and ridges – referred to as Upper Plateau in this study (Fig. 2.4 & 2.5) comprise of the following plant communities:

(i) Montane Grassland

Closely associated with the Karoo Escarpment Grassland. A similar plant community was described by Rubin & Palmer (1996) as the *Merxmuellera disticha- Lightfootia nodosa* Montane Grassland situated at high elevation. This landscape unit represents grasslands with sparsely scattered shrubs. Historically, fire has been an important component of this ecosystem, with pyrophilic grass species predominating (Rubin & Palmer 1996).

(ii) Leegtes / wetlands

Closely associated with the Bushman Vloere and Eastern Upper Karoo. Also associated with the *Euryops annae-Elytropappus rhinocerotis* Montane Shrubland described by Rubin & Palmer (1996).

(iii) Shrub thicket

Closely associated with the Upper Karoo Hardeveld. A similar plant community was described by Rubin & Palmer (1996) as the *Euryops annae- Elytropappus rhinocerotis* Montane Shrubland, as fairly dense perennial shrub patches in confined depressions and shallow valleys in the high-altitude Montane Grassland. The Montane Shrubland appears to replace the Montane Grassland where disturbance occurred in the past, while often the more mesic nature of these habitats probably protects them from natural lightning fires that sporadically occur on these mountains. Past cultivation practices are clearly visible in some larger valleys (Rubin & Palmer, 1996).

(iv) Mountain Shrubland

Closely associated with the Upper Karoo Hardeveld. A similar plant community was described by Rubin & Palmer (1996) as the *Euryops annae-Nemesia fruticans* semi-woody Shrubland, occurring on the steep higher midslopes directly under the escarpment. It consists of rocky sandstone screes interspersed with less rocky areas, and drier areas scattered with wetter areas where the sun is absent in winter and in the afternoons. The shrubland has a high canopy cover and high plant species diversity (Rubin & Palmer, 1996).

(v) Short Shrubland

Closely associated with the Upper Karoo Hardeveld. An alike plant community was described by Rubin & Palmer (1996) as the *Eriocephalus ericoides- Pteronia tricephala* Montane Dwarf Shrubland occurring on the more open and flat areas. It is the only Dwarf Shrubland on the higher reaches (Upper Plateau) within the park.

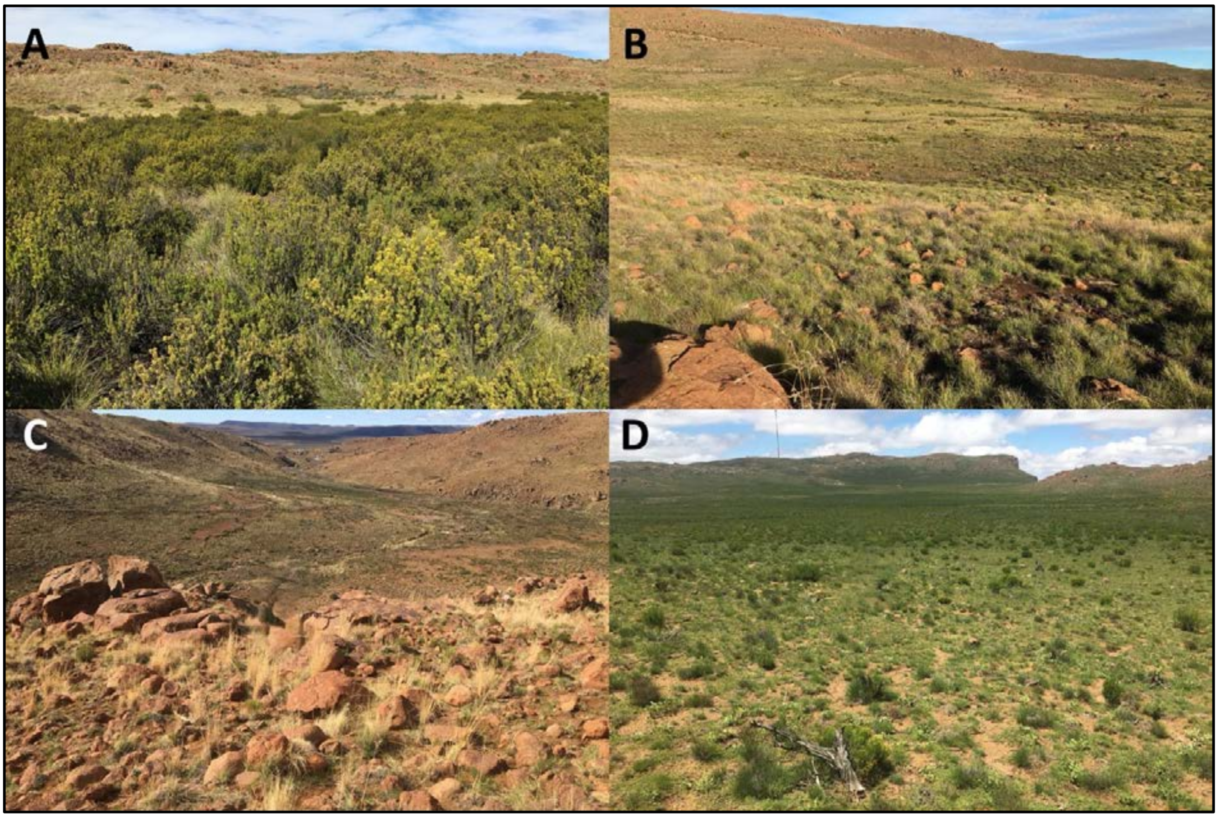

Figure 2.5 Photo representation of the Upper Plateau landscape type, displaying the general vegetation structure and terrain characteristics, within the Karoo National Park.

2. Terraces of the Nuweveld Mountain midslopes and mid-plateau – referred to as Middle Plateau in this study (Fig. 2.4 & 2.6) comprise of the following plant communities:

(vi) Grewia robusta Shrubland

An alike plant community was described by Rubin & Palmer (1996) as the *Rhigozum obovatum-Garuleum bipinnatum* Dwarf Shrubland occurring on steep, unstable to stable mudstone/sandstone midslopes, with the irregular influence of dolerite.

(vii) Grassland

This is a new landscape unit that requires more fieldwork and research before comprehensive description.

(viii) Karroid Grassland

An alike plant community was described by Rubin & Palmer (1996) as the *Eriocephalus ericoides-Trichodiadema setuliferum* Dwarf Shrubland, occurring in repetitive patterns on the flat sandstone pediments present in varying amounts on the mountain midslopes and foothills.

(ix) Searsia sparse Shrubland

An alike plant community was described by Rubin & Palmer (1996) as the *Aristida diffusa-Rhus burchellii* Grassy Shrubland occurring on the, generally flat, middle escarpment. The high shrub and grass component suggests a mesic site, probably due to the greater precipitation deposited by the south westerly fronts (Rubin & Palmer, 1996).

In terms of the Mucina & Rutherford (2006) vegetation map for SA, all four of the terraces landscape units are closely associated with the Upper Karoo Hardeveld and small isolated pockets of Gamka Karoo vegetation types.

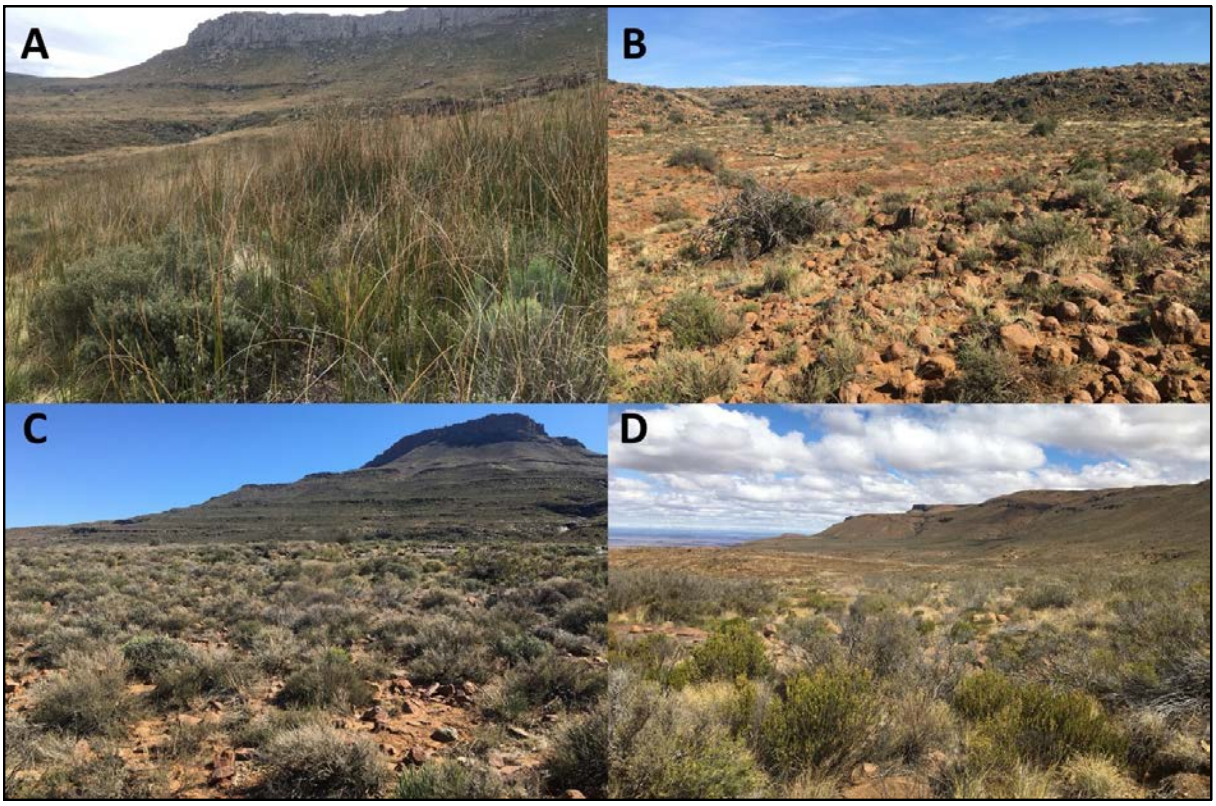

Figure 2.6 Photo representation of the Middle Plateau landscape type, displaying the general vegetation structure and terrain characteristics, within the Karoo National Park.

3. Valley bottomland– referred to as Lower Plateau in this study (Fig. 2.4 & 2.7) comprise of the following plant communities:

(x) Bossieveld

An alike plant community was described by Rubin & Palmer (1996) as the *Rhigozum obovatum-Enneapogon desvauxii* Dwarf Shrubland occurring on the foothills.

(xi) Sparse bossieveld

An alike plant community was described by Rubin & Palmer (1996) as the *Stipagrostis obtusa-*

Rhigozum obovatum Dwarf Shrubland, occurring in the lower more arid and degraded rocky footslopes and plains of Lammertjiesleegte, Sandrivier and Doornhoek.

(xii) Salsola veld

An alike plant community was described by Rubin & Palmer (1996) as the *Lycium cinereum-Salsola aphylla* Shrubland, occurring in flat, low-elevation floodplain areas. Leaching of salts and salinization of the soil is an integral part of the patterns and processes in these areas. Symptoms of erosion are conspicuous in localised areas, with brackish bare patches or deep gullies visible in some floodplains (Rubin & Palmer, 1996).

(xiii) Leegtes / Depressions / wetlands

Closely associated with the Southern Karoo riviere. Further fieldwork is required for a more detailed description.

(xiv) Thornveld

According to Bezuidenhout (2016) the thornveld lacks data for a through description and it requires further fieldwork.

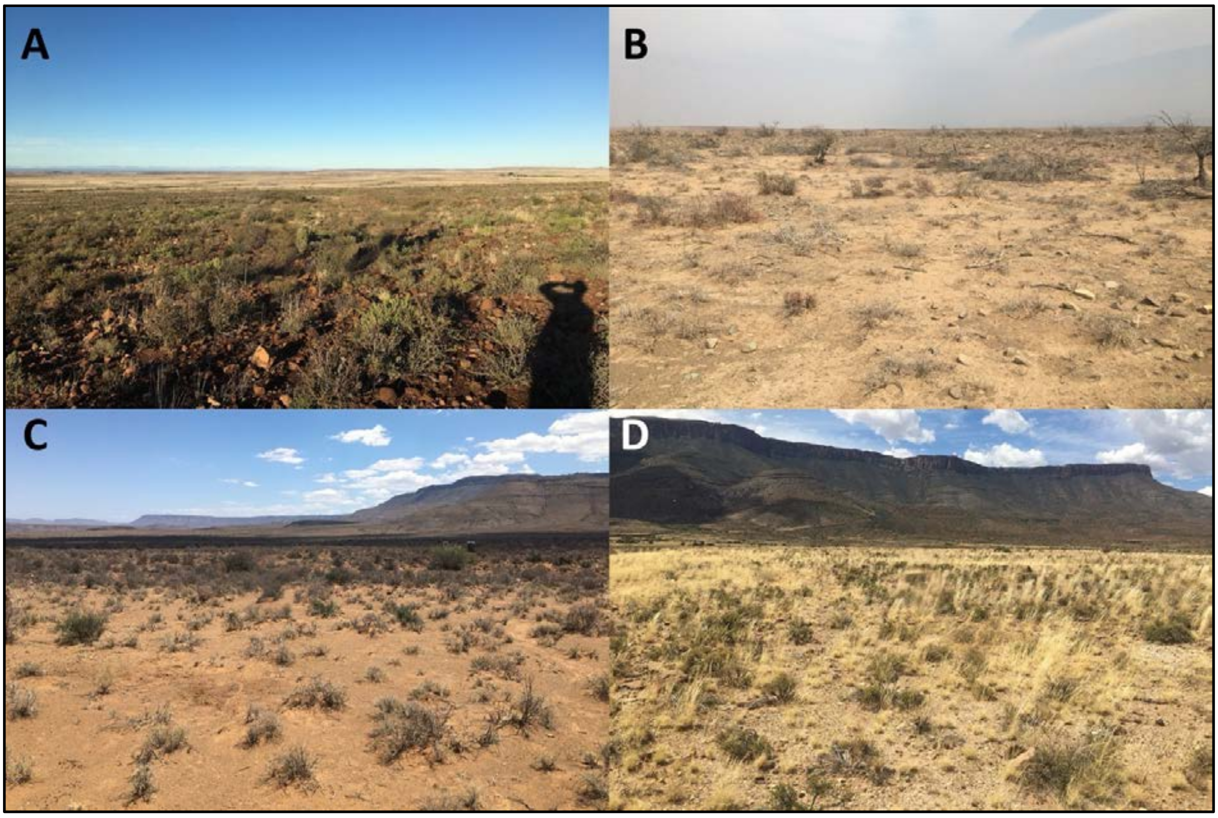

Figure 2.7 Photo representation of the Lower Plateau landscape type, displaying the general vegetation structure and terrain characteristics, within the Karoo National Park.

4. Woodland – known as Drainage Line Woodland in this study (Fig. 2.4, 2.8 & 4.1).

   A similar plant community was described by Rubin & Palmer (1996) as the *Acacia* (now *Vachellia*) *karroo-Stipagrostis namaquensis* Riparian Woodland, closely associated along the major drainage lines or rivers. This landscape unit is often the only densely vegetated area, and provides refuge and palatable browse for black rhinoceros (*Diceros bicornis bicornis*), kudu (*Tragelaphus strepsiceros*) and eland (*Tragelphus oryx*) (Rubin & Palmer, 1996).

   All the landscape units are closely associated with the Gamka Karoo vegetation type."

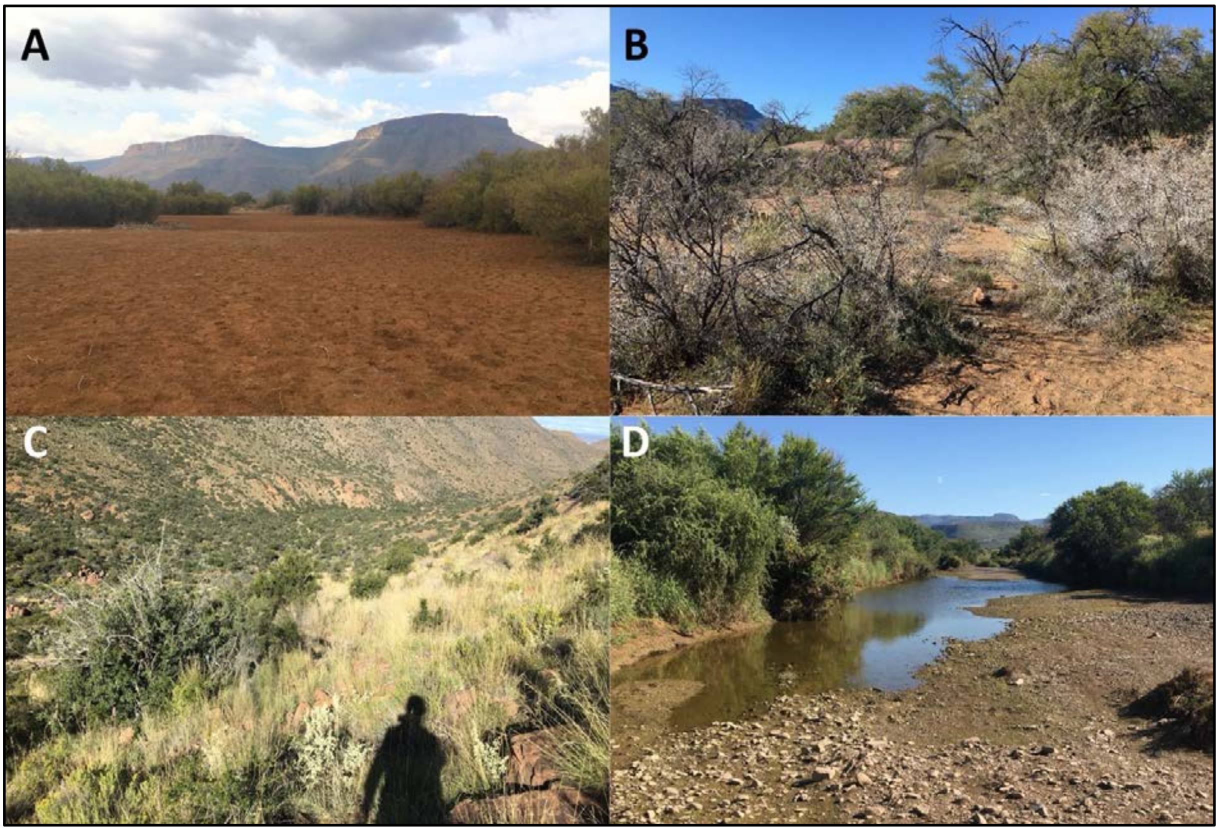

Figure 2.8 Photo representation of the Drainage Line Woodland landscape type, displaying the general vegetation structure and terrain characteristics, within the Karoo National Park.

2.9 Fauna

The KrNP contains a large variety of endemic wildlife, especially small reptiles (Spies, 2017). Throughout the greater karoo, including the KrNP, the historic enormous migratory herds of springbok (*Antidorcas marsupialis*) known as the "trekbokke", black wildebeest (*Connochaetes gnou*), Ostrich (*Struthio camelus*) and quagga (*Equus quagga quagga*) will likely never be as significant as documented in the 1800s (Spies, 2017). However, the park still hosts 57 mammal species (Appendix A), over 200 bird species and a rich reptilian count, including 18 snake species and five tortoise species – the highest density of tortoise species in the world (Spies, 2017). Mammal species, larger than five kilograms, occurring within the KrNP include herbivores; black rhinoceros, zebra (mostly Cape Mountain zebra *Equus zebra zebra*, with a few plains zebra *Equus quagga burchelli*), common duiker (*Sylvicapra grimmia*), eland, gemsbok (*Oryx gazella)*, grey rhebuck (*Pelea capreolus*), klipspringer (*Oreotragus oreotragus*), kudu, mountain reedbuck (*Redunca fulvorufula*), red hartebeest (*Alcelaphus buselaphus caama*), springbok, steenbok (*Raphicerus campestris*) and porcupine (*Hystrix africaeaustralis*)*,* carnivores; African wildcat (*Felis lybica*), bat-eared fox (*Otocyon megalotis*), brown hyena (*Parahyaena brunnea*), Cape clawless otter (*Aonyx capensis*)*,* Cape fox (*Vulpes chama*), caracal (*Caracal caracal*), lion (*Panthera leo*), omnivores; chacma baboon (*Papio ursinus*), vervet monkey (*Chlorocebus pygerythrus*) and insectivores; aardwolf (*Proteles cristata*) and antbear (aardvark) (*Orycteropus afer*) (Skinner & Chimimba, 2005, Spies, 2017; SANParks, 2024). Of the bird species present only the Common Ostrich and Kori Bustard (*Ardeotis kori*) can realistically be considered as potential lion prey. In order to re-establish species that had been eradicated but historically occurred in the region, species such as lion, brown hyaena, black rhino and Cape Mountain zebra have been reintroduced to the park in the more recent years (Spies, 2017). The reintroduction of lion and brown hyaena in 2010, in addition to their intrinsic species value, re-established their vital predation and scavenging roles in the ecosystem (Ferreira *et al.*, 2011; Codron *et al.*, 2018). The Cape mountain zebra, a species that was previously endangered, are now least concern, population within the KrNP is thriving and currently is the second largest population in South Africa (Spies, 2017). The removal of plains zebra from KrNP began in 2015, and is ongoing, after evidence was found in Mountain Zebra National Park of hybridization with Cape mountain zebra (Spies, 2017). The KrNP contributes significantly to the national conservation targets of the south-western subspecies of south-western black rhino (Ferreira *et al.*, 2016). Insects that can have profound periodic effects on the area, and its soils, are brown locust (*Pardalina locustana*) and Karoo caterpillar (*Loxostege frustalis*) that can have seasonal outbreaks. Harvester termites (*Baucaliotermes hainesi*), and harvester ants (*Messor capensis*) acts as soil engineers (Spies, 2017).

2.10 Infrastructure

The park is situated close to the N1 highway and most of its guests use it is a convenient stopover *en route* between Gauteng and Cape Town. The KrNP received 40 548 visitors in the 2015/2016 (Spies, 2017). The KrNP has one rest camp, with accommodation and camping facilities, approximately 6 km from the N1 on the old Stolzhoek farm (Spies, 2017). The camp has 37 accommodation units and 24 camping and caravan sites located within the main rest camp. Additionally, there are two remote overnight cottages and an environmental education centre in the western regions of the KrNP (Fig. 2.9 - Spies, 2017). There are two picnic sites situated along the park's road network, which includes

30 km of tar, 143 km of gravel roads and 6 km of exclusive 4x4 trails (Spies, 2017).

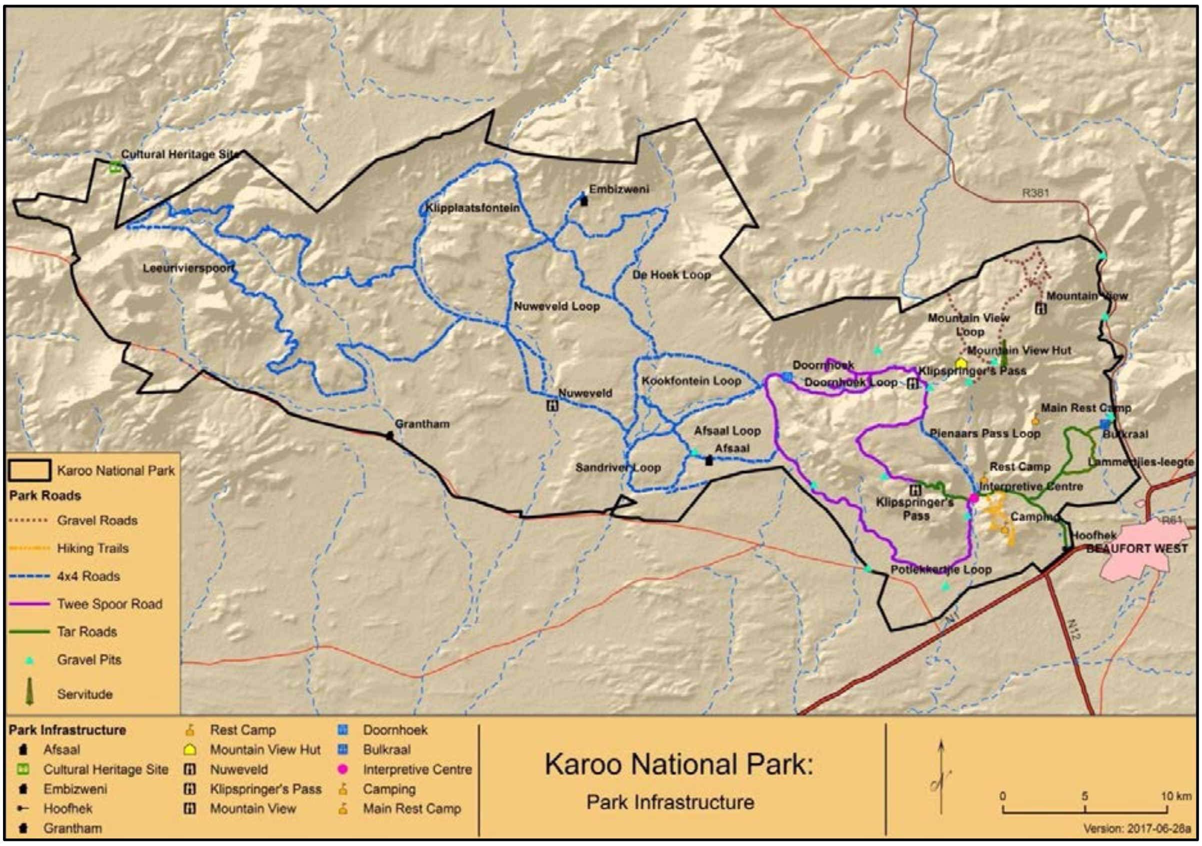

Figure 2.9 Map of the Karoo National Park depicting the parks infrastructure (SANParks Scientific services).

2.11 Surrounding land use and human impact

The park occurs in the Western Cape within the Central Karoo District Municipality (CKDM) which includes the Local Municipalities of Beaufort West, Laingsburg and Prince Albert (Spies, 2017). The reserve rest camp and head office is just 12 km from Beaufort West, a town with a significantly high unemployment percentage of 32%, and approximately 48% of the surrounding population receive government grants, thus creating a great issue for the district's municipality and KrNP (*Spies, 2017*). The Central Karoo contains limited natural resources other than sparse grazing which contributes to the agrarian economy (Spies, 2017). Agriculture and construction, light industry and their related support services are the dominant industries of the Beaufort West region (Spies, 2017) The park is bordered largely by private farms that focus on livestock, moslty lamb and less so beef, production (Spies, 2017; Hoffman *et al.*, 2018). The surrounding farms predominantly generate their power from generators, solar and wind power to generate their energy (Spies, 2017).

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CHAPTER 3

RECENT AND HISTORIC DIET OF LIONS IN KAROO NATIONAL PARK

3.1 Introduction

African lion (*Panthera leo*) functions as a flagship species for terrestrial biodiversity conservation (Loveridge *et al.,* 2009), and as apex predators, play a critical role in the ecosystem functioning (Mills *et al.,* 1978; Lindsey *et al.*, 2017). Nonetheless, the African lion is globally categorised as vulnerable on the International Union for Conservation of Nature Red List (IUCN, 2024) and inhabits only 8% of its historical range (Bauer *et al.*, 2016; Sargent *et al.*, 2021). Only the southernmost countries – Namibia, Botswana, Zimbabwe and South Africa are not experiencing population declines (Bauer *et al.,* 2015).

Although, most lions in South Africa were eradicated from their historical range by the 1900's (Nowell & Jackson, 1996) populations, persisted in the Kruger National Park (Ferreira & Funston, 2010), the Kgalagadi Transfrontier Park (Castley *et al.,* 2002; Funston, 2011) and Greater Mapungubwe Transfrontier Conservation area (Miller *et al.,* 2013). Since 1958, approximately 500 lions have been re-introduced in at least 45 different reserves throughout South Africa (Miller *et al.,* 2013). This has grown to 59 reserves where 748 lions were present in 2018 (Sellier *et al.,* 2024). It is argued, by some, that these small and isolated populations, like that of Karoo National Park (KrNP, 88 307 ha), are of minimal conservation value due to the reduction of variable genetics (Slotow & Hunter, 2009). However, more recent results have displayed that these fragmented populations have been effective at conserving lions on a broad scale (Sellier *et al.,* 2024).

Within South Africa, lion populations in small and confined reserves are generally managed within a meta-population management framework (Miller *et al.,* 2013; Sellier *et al.,* 2024). This framework accepts that the population is in discontinuous units that have different demographics and that there is limited, to no, dispersal between these units (Olivier *et al.,* 2009). The approach uses best practices to induce variable demographics and mimic dispersal through translocations (Miller *et al.,* 2013), guided by the social dynamics of lions (Ferreira & Hofmeyr, 2014) and resultantly, is one of the largest lion conservation units in Africa (Sellier *et al.,* 2024).

Within this context, lions were re-introduced into the KrNP near Beaufort West in the Western Cape in 2010 (Spies, 2017a). The regional ecologist of the KrNP states that since the re-introduction, the predation role of lion has not adequately been restored to date as animal numbers still need to be controlled, and that social constraints and pressures have been observed (Bissett *et al.,* 2021). Since reintroduction, a minimum of nine escapes events involving thirteen different lions have occurred, some of which travelled over 300 km and took 22 days to recapture (Spies, 2017a; Spies, 2017b). Escapes increase tension with the surrounding livestock farming communities and stakeholders and, ultimately, jeopardise the conservation efforts of the park (Hunter *et al.*, 2007; Packer *et al.,* 2005; Kettles and Slotow, 2009; Spies, 2017b).

Managing lion populations and associated re-introduction and removals within small reserves is complex (Miller *et al.,* 2013, Le Roux *et al.,* 2019) as they are highly vulnerable to anthropogenic factors (Herrmann, 2004) and environmental fluctuations (Bauer *et al.,* 2005). This is due to the relative low population sizes, the typical isolation of these small reserves, and for certain populations like that of KrNP, the arid and resource-poor environment in which the re-introductions occur (Mills *et al.,* 1978, Castley *et al.,* 2002). Additionally, a major challenge in managing lions in small areas is the lack of natural regulation of population sizes (Miller *et al.,* 2013). This may carry consequences for predator-prey dynamics (Tambling & du Toit, 2005; Owen-Smith & Mills 2008; Slotow & Hunter, 2009; Hayward & Kerley 2009). Furthermore, there is a lack of existing knowledge and information on lion ecology within semi-arid regions in general (Stander, 1992b; Smith, 2004; Davidson *et al.,* 2013; Beukes *et al.,* 2017), and especially so for KrNP.

In larger reserves, that are less affected by disturbance, lion populations are often self-regulating due to their social dynamics and pressures (Miller *et al.,* 2013). However, in small reserves with few rival prides and small prides the dominant males have little competition and are thus the major force and influence for a long period (up to 10 years), as opposed to larger reserves where their dominance tenure is generally short (Bygott *et al.,* 1979; Miller *et al.,* 2013; Miller & Funston, 2014). Thus, there is less infanticide and lions often overpopulate rapidly, which requires regular intervention (Lehmann *et al.,* 2008; Mosser & Packer, 2009; Miller *et al.,* 2013; Miller & Funston, 2014; McEvoy *et al.,* 2021). Approximately 87% of lion cubs survive in small reserves (Druce *et al.,* 2004; Kilian & Bothma, 2003; Lehmann *et al.,* 2008; Miller & Funston, 2014), as opposed to between 40% and 59% in larger reserves (Eloff, 1980; Lehmann *et al.,* 2008; Funston *et al.,* 2003, Funston, 2011). Furthermore, these cubs in small reserves have limited dispersal opportunities when reaching sub-adulthood (Miller *et al.,* 2013).

Resultantly, in fenced reserves lion numbers often increase to unnaturally high numbers (Power, 2002; Tambling & du Toit, 2005). These unnaturally high numbers can cause the lions to be closer to, or above, the carrying capacities that will be realised in unfenced populations and populations occurring in larger reserves (Packer *et al.,* 2013). The increase in lion numbers, in turn, can constrain prey population numbers (Power 2002a; Tambling & du Toit, 2005). Disrupted prey dynamics (Miller *et al.,* 2013; McEvoy *et al.,* 2021) and low prey availability or abundance (Lehmann *et al.,* 2008; Hayward *et al.,* 2007; Power, 2002; Tambling & Du Toit, 2005; Slotow & Hunter, 2009; Rigino, 2015) within a reserve could lead to lions searching for prey outside the fenced reserves. Furthermore, social pressures can force young male lions, or less dominant prides, to suboptimal areas of the reserve, with less prey and stalking cover, in order to avoid conflict (Lehmann *et al.,* 2008; Loveridge *et al.,* 2009; Miller *et al.,* 2013). This added pressure can then add further motivation for lions to search for prey outside the fenced reserves (Lehmann *et al.,* 2008; Loveridge *et al.,* 2009; Maruping-Mzileni *et al.,* 2017).

Dietary profiles assist in understanding predator-prey demographics (Owen-Smith & Mills, 2008) and lion population dynamics (Becker *et al.,* 2013), which in turn can inform management decisions. Although lion diet estimates and preferences are comprehensively reviewed (Schaller, 1972; Bryden, 1978; Viljoen, 1993; Power, 2002; Power, 2003; Hayward & Kerley, 2005; Davidson *et al.,* 2013; Miller *et al.,* 2013) there has been limited research in arid to semi-arid environments (Stander, 1992b; Smith, 2004; Davidson *et al.,* 2013; Beukes *et al.,* 2017). Within the KrNP, it is unclear what the diet of lions is, whether it changes over time, and whether present dietary needs and constraints provide motivation for lions to search for prey beyond the boundary of the park.

Here I focus on improving our understanding of lion feeding habits in the KrNP using prey records obtained from location data sourced from GPS collars fitted to lions within the park for monitoring and management purposes. Lion GPS location points recorded over a short period within close proximity to each other (commonly known as GPS clusters) help identify the location of lion feeding events (Merrill, *et al.,* 2010; Pitman *et al.,* 2012). A detailed inventory of recent lion diet was created by doing intensive monthly searches of lion GPS clusters between 2021/2022 which was then compared to lion kill records collated by park personnel from 2010 – 2020 in a similar but less intensive and structured manner.

My first objective was to use the recent diet data to obtain a clear and accurate understanding of KrNP lion diet and prey preference which can inform on whether the abundance of certain key prey species might act as incentive for lions to leave the park. The second objective was then to use the comparison of the recent and historic dietary data to establish whether prey use and preference change over time as some dietary plasticity might mitigate perceived key prey species shortages. Newly introduced lions could favour certain species linked to what they were used to and favoured at the locality where they came from, or they could randomly choose prey species based on what they encounter while doing exploration of new territories that they are forced to use (Hayward *et al.,* 2011). Perturbations and conditions that lions encounter, however, can induce prey switches as seen in Kruger National Park (Maruping-Mzileni *et al.,* 2017) and Eastern Cape (Bisset, 2012).

I acknowledge that dietary data sourced from GPS cluster analysis is biased towards larger prey items (Tambling *et al.,* 2012, Beukes *et al.,* 2017). However, since lions prefer large prey species, irrespective of their availability, within a weight range of 190 to 550 kg (Hayward & Kerley, 2005) and that, when available, large prey provide the vast majority of biomass consumed (Beukes *et al.*, 2017) this approach was considered the most appropriate to use. The study is thus restrict to the use of large prey items (> 50 kg) by lion.

3.2 Methodology

3.2.1 Study area

KrNP, covers 883 km^2 (Saayman *et al.,* 2009; Spies, 2017a) and is located between 32°10’S-32°23'S and 22°15'E-22°35'E (Rubin *et al.,* 2001). The study focused on the eastern portion (approximately half) of the park due to accessibility and logistical constraints, but provided a representative sample of the reserve’s four broad landscape types and was also the area the majority of lions utilised during the time of the study (Fig. 2.1).

The KrNP receives predominantly summer rainfall and has a mean annual rainfall that varies significantly throughout the park ranging between 175 mm, in the East, to 406 mm, in the West. Most rain (60% – 75%) is in summer (Rubin *et al.,* 2001; Spies, 2017a). The KrNP experiences cold winters, with a mean minimum winter temperature of 3.5 °C, and hot summers, with a mean maximum summer temperature of over 32 °C.

Specifically, within the study site, the average rainfall for the area is 287 mm (Fig. 2.2, Moeletsi *et al.*, 2022). Over the 12-year study period, the rainfall averaged 289 mm per annum and fluctuated between 495 mm and 118 mm (Moeletsi *et al.*, 2022). The period between 2015 to 2019 was particularly dry, resulting in a drought, with an average of 178 mm, a maximum of 210 mm and a minimum of 118 mm, hitting its peak drought in 2019 (Moeletsi *et al.*, 2022).

The mountains within the park form part of the Great Escarpment which differ significantly in elevation from 820 – 1 620 masl (Fig. 2.3, Spies, 2017a). The park's contrasting elevation has a marked influence on the climate, with a cool steppe climate and it’s associated steep elevation and a precipitation gradient rapidly changing to a warm steppe climate in the eastern, southern and western lowland sections of the park (Spies, 2017a).

The park hosts 58 mammal species (Spies, 2017a). Mammal species include plains game typical of the Karoo landscape, these include (in order of abundance) gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus caama*), springbok (*Antidorcas marsupialis*), Cape mountain zebra (*Equus zebra zebra*), greater kudu (*Tragelaphus strepsiceros*), common eland (*Tragelaphus oryx*), ostrich (*Struthio camelus*), grey rhebok (*Pelea capreolus*) and plains zebra (*Equus quagga*) (Spies, 2017a).

Additionally, less commonly found smaller mammals include Chacma baboon (*Papio ursinus*), Cape porcupine (*Hystrix africaeaustralis*) and warthog (*Phacochoerus africanus*).

The KrNP is situated in the semi-arid Nama-Karoo and along the Nuweveld Mountain range (Kraaij & Milton, 2006; Spies, 2017a). The vegetation of the park falls within two Biomes, namely; the Nama-Karoo, which covers the majority of the park and a relatively small portion of the Grassland Biome (Kraaij & Milton, 2006; Spies, 2017a; Bezuidenhout *et al.,* 2024). Structurally, the vegetation is characterised largely by low-lying shrubs, sparse tree and grass cover on the slopes and open plains, and thicker riparian vegetation and trees in the riverbeds and valleys (Kraaij & Milton, 2006; Spies, 2017a; Bezuidenhout *et al.,* 2024).

The vegetation of the KrNP can be divided into four broad landscape units that are largely defined by the associated elevation and gradient. The 4 landscape types are; the Nuweveld Mountain plateau and ridges, Terraces of the Nuweveld Mountain mid-slopes and mid-plateau, the valley bottomland, and the drainage lines dissecting the bottomland. These units can be further subdivided into 11 different sub-communities (Bezuidenhout, 2016). A more comprehensive account of the biotic and abiotic features of the KrNP and study area has been described in Chapter 2.

3.2.2 Prey abundance

Prey species distribution and availability were taken from annual aerial census data provided by SANParks (Bissett *et al.,* 2021). An annual aerial census is done as mandated by the parks management plan and was completed every year between 2010 and 2021 except in 2020 due to budget constraints and COVID-19. Aerial Transects of 400 m wide (200 m strips on either side of the helicopter) are flown across the entire park over five days. The surveys started in the mountainous areas in the north-eastern section of the KrNP and continued west, flying east-west transects across the park, with contours being flown along the high mountain ranges with steeper terrain. The counts were conducted by rangers and the regional ecologist from an approximate height of 200 ft flying at an average speed of 80 km/hr along the predefined transects. All animals seen were counted and, where required, herds were flushed to ensure a robust count. Where large herds of animals were identified, the helicopter circled to allow observers to record all animals in the group. All data was recorded on a laptop computer using a software programme called Colibri that obtained the GPS coordinates from a linked GPS (Bissett *et al.,* 2021).

The proportional availability of prey numbers, counted during annual aerial census, was calculated by taking the number of a particular species counted and dividing that by the total number of large prey animals counted. The proportions were calculated for the six large prey species (> 50 kg).

3.2.3 GPS cluster analysis

Global Positioning System (GPS) cluster methods are becoming more commonly used to locate feeding sites for large carnivores, due to their cost and timeous efficiency (Tambling, 2010; Tambling *et al.,* 2012). Within this study, GPS cluster analysis was done through physical kill site cluster (GPS location) visitation. The kill site GPS locations were historically (2010 – 2020) identified by rangers scrutinising the location points plotted on a map by eye, while the more recent kill sites (2021/2022) were located using a mathematical model that identified sites more accurately and robustly.

The VHF and IR-SAT collars (African Wildlife Tracking^{cc}, Pretoria, South Africa) used provide multiple location points daily and allow for known individuals and their associated prides to be observed on a regular basis (Pitman *et al.,* 2012) that make it possible to quickly locate and return lions to the park in the case of breakouts from the park. The collaring of lions forms part of the carnivore lion management programme of SANParks (Spies, 2017a). Permission was granted by SANParks (Permit. Number: RADL-F/2021-04) to access the GPS information collected from fitted collars. My focus was on using the information to identify kill sites.

3.2.4 Lion diet defined using cluster analysis

For this study, information on lion diet were obtained from the visitation of lion kills sites which was identified using GPS clustering analysis (Anderson & Lindzey, 2003; Tambling *et al.,* 2012). Lion dietary data for the years 2010 – 2020 was extracted from monthly ranger reports where they detailed their findings from visiting lion GPS clusters. Although the visitation of clusters was part of the monthly duties of rangers the identification of such clusters were made in a subjective and none rigorous manner, with visits to sites dictated by logistical and financial constraints. This ranger collated data set is further referred to as the historic lion diet data set. Information on the more recent diet (2021 and 2022) was also obtained from the visitation of lion GPS clusters, but the identification of potential lion kill clusters and the visitation of these locations was done in a much more objective and systematic manner. The more recent diet data set is referred to as the contemporary lion data set. The collation of both data set is explained in more detail below.

3.2.4.1 Contemporary lion diet

The contemporary diet of lions was intensely studied between the months of March 2021 to May 2022 by searching for prey remains at sites where lions spent prolonged periods of time. The lions' movements and sites where lions spent prolonged periods of time were identified using the GPS collar data.

During the 15-month study period, the estimated lion population was 11 individuals (two males and nine lionesses) of which eight were collared (two males and 6 lionesses) and they had equal and unrestricted access to the entire reserve and hence the study area (Fig. 3.1). The lions to be collared are carefully selected by SANParks staff to ensure that at least one lion per known grouping, or pride, is collared so that they have a good idea where most lions are all the time. During the study period at least one individual from each of the six known social groupings within the KrNP, was collared.

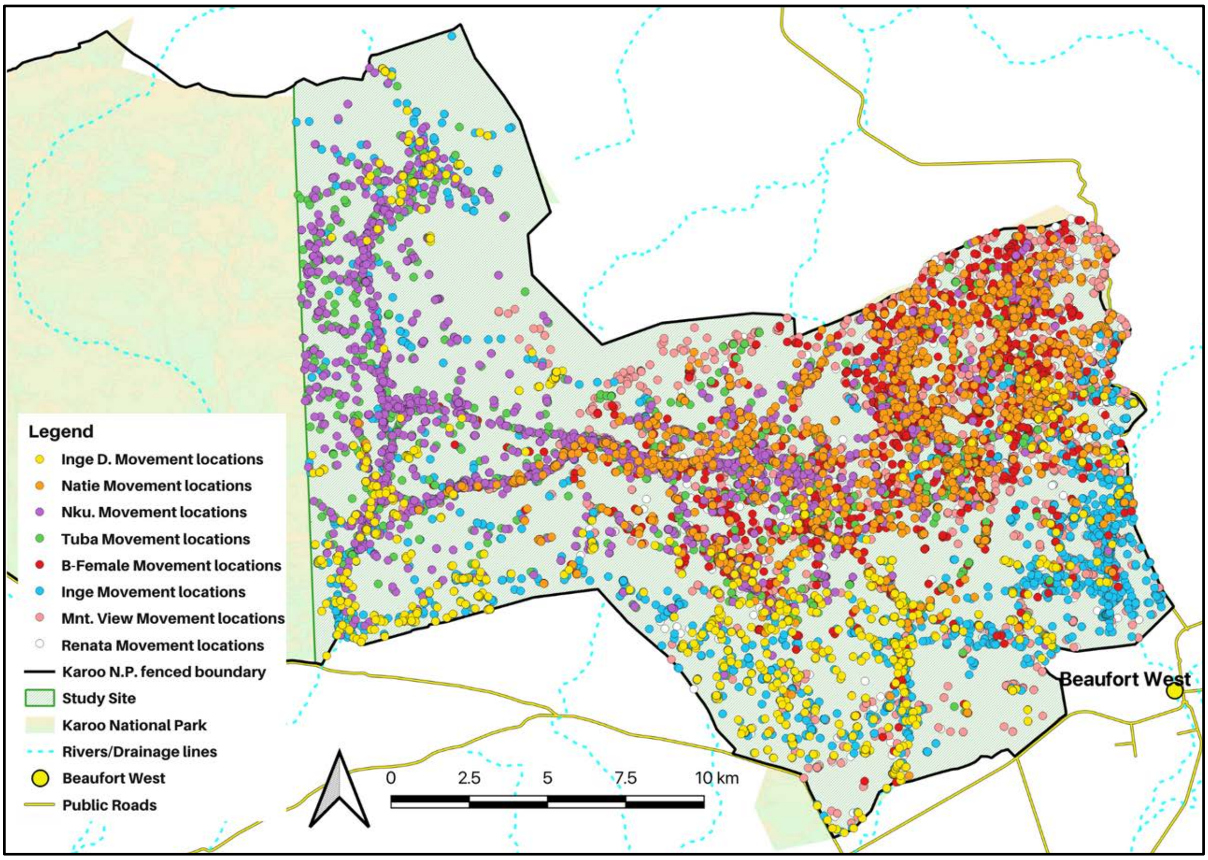

Figure 3.1 A map of the study area within KrNP indicating the location points downloaded from the GPS satellite collars fitted to eight lions between March 2021 and May 2022. The names used by park staff for the respective lions are provided in the legend together with the colour associate with the location point indicated for each individual.

The GPS satellite collars were set to record eight lion localities daily - six during the evening and night-time (17:00-5:00), at 2 hr intervals, and two fixes during the daytime (5:00-17:00), at 6 hr intervals. The GPS data points signalled by the collars provide detail on the location and movement of the collared individuals over time (Sand *et al.,* 2005; Tambling, 2010). A concentration of two or more consecutive GPS fixes within a 100-meter radius, were considered a cluster point (Tambling *et al.,* 2012). Clustering is most noticeable two hours after a kill (Tambling & Belton 2009).

Clusters for investigation were prioritized based on the following criteria. Firstly, we investigated the ratio of distance moved in the 24 hours prior to the cluster formation against the distance moved in the 24 hours after moving away from the cluster (called R24), with a higher ratio depicting movement (searching for food) prior to a cluster and resting (sleeping after feeding) following a cluster (Tambling et al. 2012). Secondly, we prioritised clusters where lions had remained at the location for a longer period of time, increasing the likelihood of there being a feeding event (Tambling et al. 2012). Finally, we prioritised clusters that start during the night compared to those that start during the day due to lions hunting more at night (Tambling et al. 2012).

For this study, cluster investigation was prioritized for clusters that were predicted to be the result of a kill. We separated the clusters that were likely to be a kill into those where we were more confident ("likely clusters") and those that we were less confident ("potential clusters"). A "Potential cluster" was defined as a cluster that had a R24 ratio of ≥ 3 and duration time ≥ 8 hours and being formed during the night. A "Likely cluster" was considered as a cluster that had a R24 ≥ 10 and duration time ≥ 12 hours and being formed during the night. All potential and likely GPS Clusters were visited while clusters occurring outside of these parameters were largely excluded from investigations (Fig. 3.2). Some clusters occurring outside of these parameters were visited if either R24 or duration was high (and the other not) and the cluster was relatively easily to access (i.e. *en route* to another kill site and/or close to road access). The clusters that were created in the daytime were largely disregarded unless the R24 and duration stats suggested a likely kill site.

The first GPS location point of an identified cluster was used as the start of the search pattern for searching for prey remains. The respective GPS points that made up the cluster were loaded onto a handheld GPS unit (Garmin E-Trex, Garmin International, Olathe, KS, USA), with their corresponding point name, to facilitate locating the identified clusters in the field. The clusters were visited on an average of 33.5 days (range 1-126 days) after the cluster formation with 56% visited within 30 days of formation. The GPS points were deemed relevant and worth visiting if they were more recent than 60 days, or if they were a highly likely cluster that was older than 60 days (this was during the initial period of the study when some of the cluster sites were older and hadn't been visited previous to the study). Cluster locations were tracked to by road, as far as possible, and then by foot. The area around the identified location point of a cluster was exhaustively searched, irrespective of time taken, within a 100 m radius, for evidence of prey remains (Tambling *et al.,* 2012; Sand *et al.,* 2005) and this was generally done using a spiral walking pattern.

A feeding event site was confirmed if either a carcass, or parts thereof (such as rumen content, hair, bone, jaw, horn or blood) were found or evidence of lion activity, such as irregular soil disturbance and trampled vegetation as a result of a struggle or feeding frenzy (Pitman *et al.,* 2012; Davidson *et al.,* 2013). The evidence was used to classify prey according to species and where possible age and sex (Tambling *et al.,* 2012).

3.2.4.2 Historic lion diet

Since the reintroduction of lions to KrNP in 2010, park management have made an effort to collar at least one member of each lion pride with satellite enabled location collars. Between 2013 and 2021, an average of 7.22 lions were fitted with collars per year, with a maximum at one time of 11 in 2016 and a minimum of one in 2020.

After the lion reintroduction, the KrNP rangers have been keeping track of lion prey use using GPS collar location data to identify clusters and thus potential kill sites. The clusters were identified by rangers manually in a subjective manner by ”eyeballing” plotted location points that was close to each other and easily accessible from roads. It was done as part of routine operations and there was variation in effort and success between years. These clusters were visited by field rangers and prey consumed at cluster points was identified when found. These identified kill sites were augmented with opportunistic finds of lion kills and were recorded in a “carcass register”. The carcass register was summarised in the monthly ranger reports, which was further scrutinised, and the necessary data extracted (Appendix B).

Most of the data was collated from the mentioned ranger reports but additional information pertaining to the 2011 lion diet was obtained from the research work of Dr C.J. Tambling’s (personal communication, 2021).

3.2.5 Composition and preference

Lion diet was quantified by the relative proportions, as well as the biomass contributions, of the large prey species (>50 kgs) found at the identified GPS cluster points as obtained from the contemporary and historic lion diet data sets (i.e. the number of occurrences of each prey item divided by the total sample size for each year) (Tambling *et al.,* 2010; Tambling *et al.,* 2012; Davidson *et al.,* 2013; Beukes, 2017).

The frequency of the large prey occurrence in lion diet was converted into relative biomass indices (RBI) (Beukes, 2016; Balme *et al.,* 2010). The RBI (See Appendix C) was subjectively calculated using the average adult female body weight for each species obtained from Skinner & Chimimba (2005) (Radloff & du Toit, 2004; Cumming & Cumming, 2003; Tambling *et al.,* 2012; Davidson *et al.,* 2013).

Brillouin index (*Hb*), as seen in (1), is recommended to measure the adequacy of a collection (Pielou, 1975). In this study, the Brillouin Index was used to assess whether the number of kill records collected was sufficient to portray the diet of lion accurately (Glen and Dickman, 2006):

$$Hb = \frac{\ln N! - \sum \ln n_i!}{N} \tag{1}$$

where Hb represents the cumulative diversity of prey in the collection, N is the complete number of individuals in the specific sample, n_i is the number of individuals belonging specifically to the *i*-th species (Brillouin, 1956). Cumulative diversity was calculated by bootstrapping 10,000 random samples in increments of three and plotted against the total number of collected samples. Sampling effort was deemed adequate if the diversity curve reached an asymptote and the incremental change declined to <1% (Briers-Louw and Leslie, 2020).

The Jacobs' Index, as seen in (2), was used to measure prey preference (*D*) (Jacobs, 1974; Hayward & Kerley, 2005; Rapson & Bernard, 2007; Davidson *et al.,* 2013),

$$D = \frac{r-p}{r+p-2rp} \tag{2}$$

where *r* is the proportional contribution of a species in the total lion sample and *p* is the proportional availability of that specific species. The lion feeding data obtained from the contemporary and historic collated data provided r, while p was derived from the aerial game census (Appendix D).

The Jacobs index allows for evaluating prey selection when different relative abundances of prey are compared (Jacobs, 1974). The Jacobs' index was calculated independently for the diet obtained from the contemporary data set (D_{gps}) and diet records obtained from the historic data set (D_{His}). The resulting value scores between +1 and -1, with zero indicating no selection, +1 indicating maximum preference, and -1 indicating maximum avoidance (Jacobs, 1974). Furthermore, a value between -0.2 and 0.2 indicates that the species was consumed as would be expected and in proportion to relative availability (Hayward *et al.,* 2011).

The complete set of lion dietary data was analysed to identify if there was any shifting or significant change in the diet composition over the years. The biomass contribution per species was then calculated per year.

The data was tested, using the Bray-Curtis distance analysis (or index of dissimilarity) (3), to identify if there was any data dissimilarity (Bray & Curtis, 1957; Danielsson, 1980),

$$BC_d = \frac{\sum|x_i - x_j|}{\sum(x_i + x_j)} \tag{3}$$

where BC_d is the Bray-Curtis dissimilarity score, x_i is the species counts at site *i* and x_j is the species counts at site *j*.

A stress plot was created to show the relationship between observed dissimilarity (x-axis) and ordination distance (y-axis). This plot assesses how well the non-metric multidimensional scaling (nMDS) ordination represents the dissimilarity data (Dexter *et al.*, 2018).

The nMDS Ordination plot summarize the differences (dissimilarity) in the community composition (in this case the composition of prey species consumed by lion per year) between various points (Shepard, 1962a; Shepard, 1962b; Kruskal, 1964a; Kruskal, 1964b; Shepard, 1980), and here the points reflect years. The plot simplifies complex community data into two dimensions (Dexter *et al.*, 2018). The closer the points are clustered together indicate similar species compositions, the further away (more isolated) the more unique the species composition. The vectors represent the influence of different species on the ordination and the direction and length of the vector indicate how strongly a species is associated with certain years.

Further analysis was conducted by constructing a DENDROGRAM, which is a tree-like diagram used to illustrate the hierarchical clustering of data (Gauch & Whittaker, 1981). In this study, the dendogram shows the similarity (or dissimilarity) in lion kill patterns across the different years. The significance of the dissimilarity is shown on the y-axis, the greater the length of the respective year's branches/arms the greater the difference.

All statistical procedures were conducted in R-Studio software, version 2022.07.1 (RStudio, 2022).

3.3 Results

3.3.1 Contemporary lion diet

During the 15-month study period 2 945 clusters were formed. Of these clusters 358 were identified as potential kill sites and, of those, 171 were highly likely kill sites (Table 3.1 & Fig. 3.2). Effort was made to visit all the highly likely kill sites with only 9 (5%) not visited. The 162 highly likely clusters that were visited yielded 119 yielded results, 97 kills and 22 non-kills. The remaining 43 sites were found to be "duplicates". The "duplicates" were where, the same lion created another cluster set nearby but far enough to be separate from the confirmed kill site cluster, or where two, or more, lions created clusters at the same location. Additionally, 65 potential kill clusters were visited that were logistically feasible, and 47 of those were recorded kill sites. Resultantly, 227 GPS cluster sites were visited and searched during the study (Fig. 3.2).

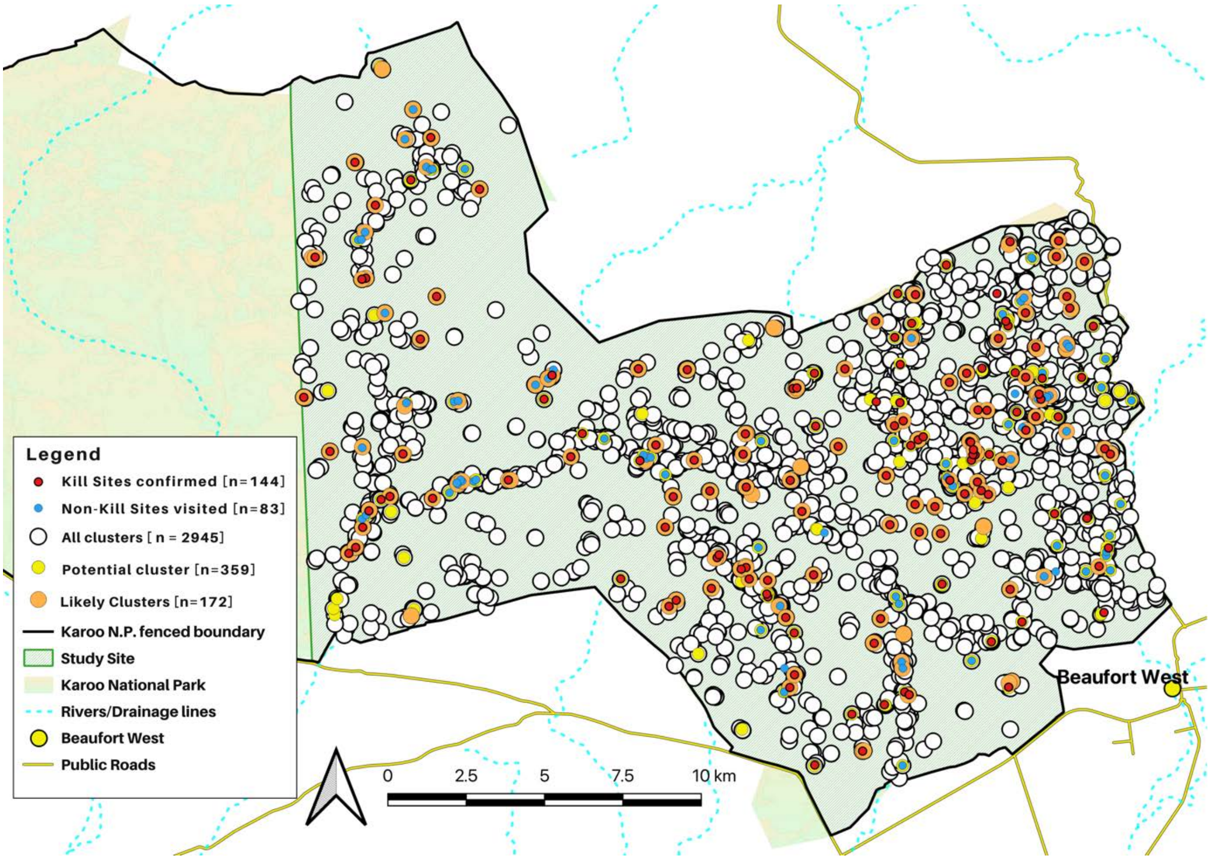

Figure 3.2 The study area in the Karoo National Park shows the GPS cluster points identified from the eight collared lions' movement data. White dots indicate all cluster points (n=2 945), yellow dots are clusters identified as "potential kill sites" (n=358), orange dots are clusters identified as "likely kill sites" (n=171), blue dots are clusters identified as potential feeding sites but with no remains/evidence found (n=83), red dots are those clusters where prey remains were found of prey (n=144) (QGIS Development Team, 2021).

***Table 3.1** A summary of GPS clusters and kill sites visit data.*

	Specifics	**Number**
Clusters	All Clusters (within study area)	2945
	Potential	358
	Likely	171
Kills Sites	Potential and likely Kill Sites Visited	227
	Evidence found	144

The Brillouin index analysis indicates that a sample of 45 kills would have been sufficient to adequately represent the lion diet of 2021/2022 (Fig 3.3a). The sample of 144 thus far exceeds the sample size for adequate sampling to help define the recent composition of large prey in the diet of lions.

At the 144 locations where lion prey remains were found, the three most commonly identified prey species were; common eland (*n*=31, 21.5%), red hartebeest (*n*=30, 20.8%) and greater kudu (*n*=28, 19.4%), these accounted for 61.7% (*n*=89) of the carcasses found during the study period (Fig. 3.3b). These were followed by gemsbok (*n*=17, 11.8%), zebra (both plains and cape mountain zebra pooled together, *n*=9, 6.3%) and ostrich (*n*=4, 2.8%). The less frequent and largely individual cases of, chacma baboon (*n*=1, 0.7%), Cape porcupine (*n*=1, 0.7%), warthog (*n*=2, 1.4%) and springbok (*n*=1, 0.7%) made up 3.5% of the diet. The prey species of 20 kill sites visited could not be identified to species level and were removed from the further analysis.

Comparatively, looking at the availability of large prey species (> 50 kg), based upon annual aerial census data from 2021 (Fig. 3.3c), gemsbok, red hartebeest and zebra were the most abundant species throughout the KrNP, contributing 68% of the available large prey species in almost equal portions. Common eland, greater kudu and ostrich contributed the remaining 32%, with eland being most abundant of the three and ostrich the least abundant.

Gemsbok and zebra contribute 45% of the available large prey (Fig. 3.3c), and yet they are less preyed upon, contributing only 18% to the large prey species killed (Fig. 3.3b). The Jacobs index scores for gemsbok and zebra is consequently also low at -0.27 and -0.54 respectively (Fig 3.3d). Conversely, eland and kudu are two of the less abundant species, contributing 25% of the available large prey (Fig. 3.3c), and yet they make up 41% of the chosen large prey (Fig. 3.3b). The Jacobs index scores of these two species are then also the highest at 0.37 and 0.42 respectively (Fig 3.3d).

During 2021/22, eland was the greatest biomass contributor to lion diet in the KrNP at 40%, followed by kudu (19%) and then equally by red hartebeest and gemsbok at 16% each. Zebra (9%) and ostrich (1%) make up the remaining large prey (2021/22 results in Fig. 3.7a).

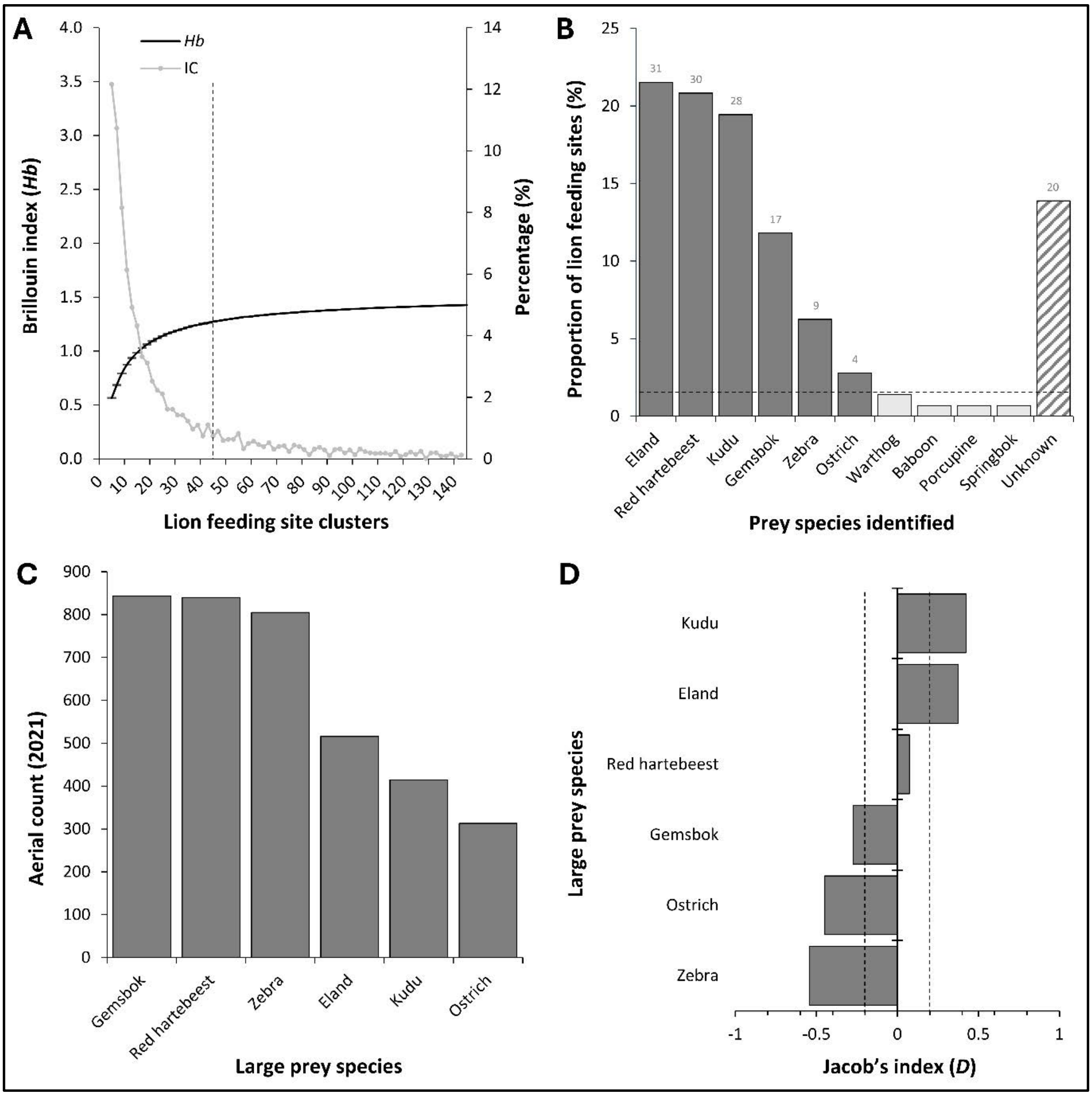

Figure 3.3 (A) Prey species rarefaction curve (Hb; mean and 95% confidence intervals; black) based on the Brillouin Index and sequential proportion of incremental change (IC; %; grey) in lion feeding sites (n = 144) as identified through cluster analyses of probable kills (n = 227) using the GPS collar data of eight lions in Karoo National Park from March 2021 to December 2022. The dashed vertical line (black) indicates the adequate sampling threshold, as the randomised sequential proportion of incremental change in prey species composition declines to <1%. **(B)** The full suite of species identified, with the number of kills of the respective large prey species and number of kill sites with unidentifiable prey remains displayed at the top of the bar. **(C)** The minimum number of individuals of prey species observed during aerial surveys in 2021. **(D)** The Jacobs index, calculated from the kill records collated from March 2021 to May 2022, and the aerial count data from the 2021 aerial census numbers.

3.3.2 Historic lion diet data and trends over time

The 1 035 carcass records obtained from the ranger reports are not evenly distributed between years (*Table 3.2*) and the kill records of 2010 (n=3) were merged with that of 2011 as lions were only introduced in November 2010. The sample sizes of recorded kills per year varied from as few as 37 in 2012 to as many as 168 in 2016. These observations did not clearly link to the number of lions known to be present at a time suggesting that observation effort varied unpredictably over time (*Table 3.2*). Brillouin's index results indicated that the years 2012 and 2020 do not have adequate samples for robust deductions and deductions on lion diet changes, for 2010/11 and 2018, should be consider carefully as the sample sizes are adequate but only just so (*Table 3.3*).

Table 3.2 *Number of lion-kill records available between 2011 and 2020 in relation to the number of lions present at the particular time.*

Year	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
No. of Kills recorded	59	37	147	116	77	168	99	61	89	43
No. of Lions	7	11	11	11	16	24	26	24	24	11

Table 3.3 *Brillouin index results for the lion kill data collated using ranger reports from the Karoo National parks, indicating the minimum sample required and the standard error (SE), for the years 2010 – 2022. Red numbers indicate samples that* do not have adequate sample size for robust deductions and orange numbers are sample sizes that are adequate but only just so.

	2010 / 11	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021 / 22**
Minimum sample required	59	67	44	46	54	37	52	58	53	64	48
SE	0.15	0.06	0.56	0.29	0.18	0.45	0.26	0.2	0.29	0.14	0.27

Proportional prey contribution over time

The large prey diet of lions, from 2010 to 2022, is largely dominated by eland (20%), kudu (26%), red hartebeest (19%) and gemsbok (23%, Fig. 3.4c). Conversely, zebra (10%) and ostrich (2%) contribute less so to the total percentage contribution (Fig. 3.4c). The yearly diet in general displays similar patterns over time but there were three clearly noticeable shifts (Fig 3.4a & b). In 2010/2011 zebra and gemsbok contributed 54% to the total diet and kudu were less fed upon (13%) in comparison to other years. In 2013 significantly more kudu was preyed upon, contributing 41% to the total diet, and eland less so (9%) in comparison to other years. In 2019, zebra and gemsbok contributed 54% to the total diet and red hartebeest contributed less than in other years (9%). In 2010/11 and 2019 zebra contributed 25% and 20% respectively, which was significantly more than most other years where zebra contributed between 5 and 8%. That said, in all other years red hartebeest, eland, kudu and gemsbok together contributed over 80% of the total lion diet.

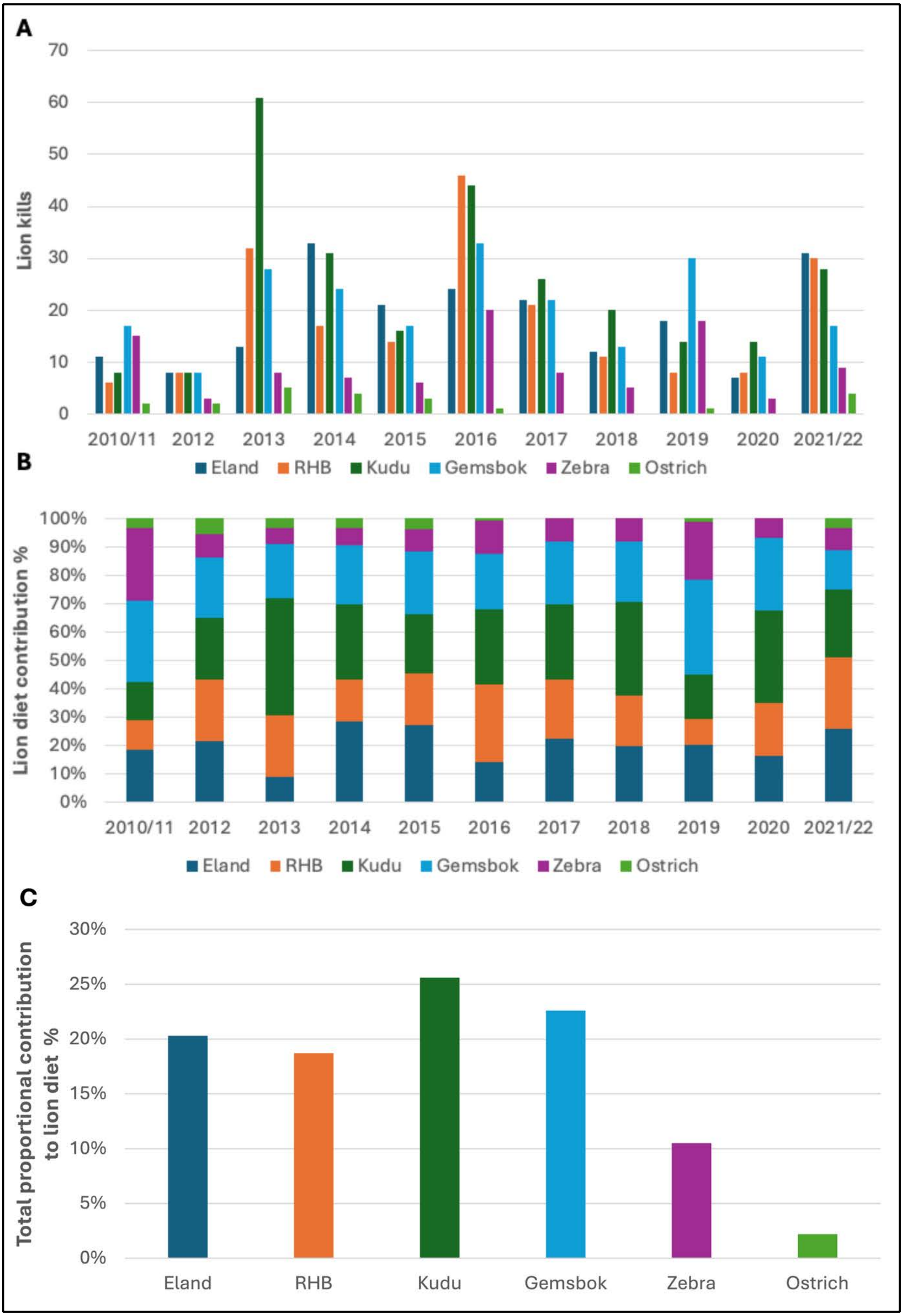

Figure 3.4 Temporal variation in lion diet from 2010 till 2022 in KrNP. **(A)** The number of kills made by lions of the six large herbivore species (>50kg) in each year. **(B)** Proportional prey consumption, of the six large main

prey species, in each year. *The 2010 and 2011 kill data were merged as too few kill sites were visited in 2010 soon after the lion reintroduction, and the kill data of 2021 and 2022 were pooled as kill data was only collected for the first 5 months of 2022. **(C)** The total proportional prey consumption, of the six large main prey species (>50kg) from 2010 till 2022.

The nMDS ordination plot that summarizes the differences (dissimilarity) in the prey species composition consumed by lions between the years (Fig. 3.5a) corroborate the identified shifts in diet over time. The stress plot (Fig. 3.9b) and associated non-metric and linear fit R² values of 0.999 and 0.997 respectively indicates an excellent match between the distances in the ordination space and the original dissimilarities, suggesting a highly accurate representation of the ecological dissimilarities.

The outlier years of 2010/11, and 2019 are years with the highest proportional consumption of zebra while 2013 have a disproportionally high consumption of kudu (Fig.3.5a). The years 2012, 2014, 2015, 2021/22 group together with the most similar prey species composition that includes all six species. The years 2017, 2018 and 2020 forms another grouping due to the lack of ostrich in the diet during those years.

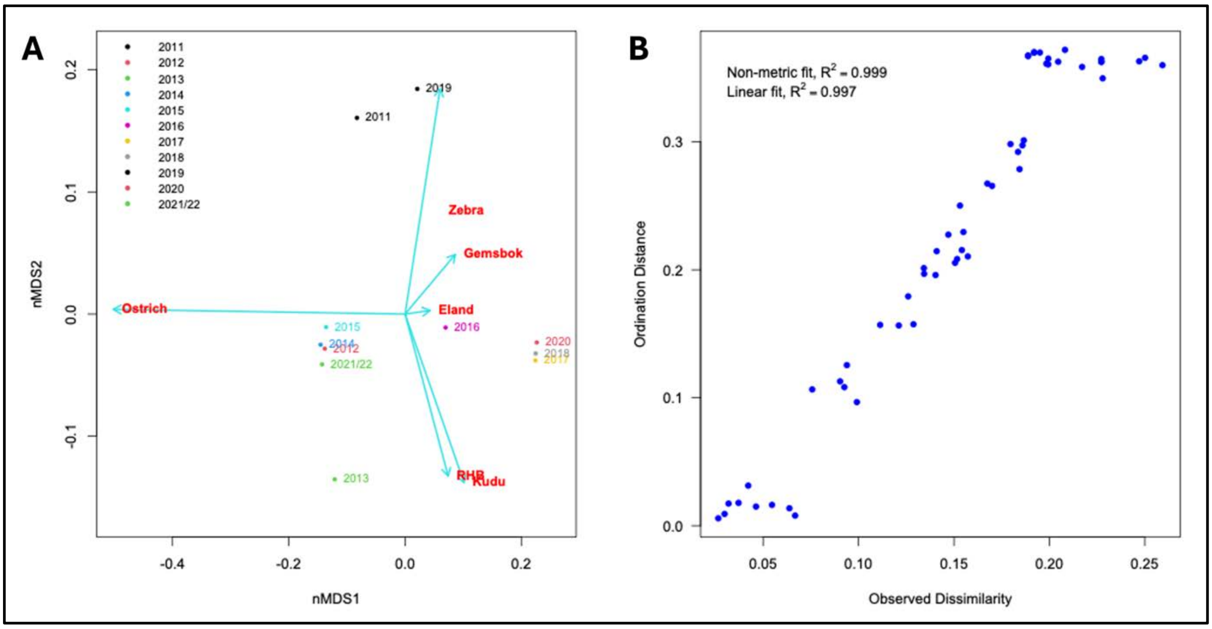

Figure 3.5 (A) An nMDS ordination plot displaying the yearly differences (dissimilarity) in the six large prey species (>50kg) composition consumed by lions from 2010 till 2022 in KrNP. Plotted in different colours are the years, and the influence of the respective species on the compositional differences are shown as vectors (arrows), labelled according to species. **(B)** The Bray-Curtis stress plot of the lion kill data pertaining to the six large prey species (>50kg) consumed each year from 2010 till 2022. The stress plot measures the ordinance distance (y-axis) and the observed dissimilarity (x-axis) to assess if the nMDS provides an accurate representation of the ecological dissimilarities. The coefficient of determination (R²) values for the non-metric fit (R²=0.999) and the linear fit (R²=0.997) are shown.

The dendrogram (Fig. 3.6), provides an additional and more refined perspective on the similarity (or dissimilarity) in lion kill patterns across the different years and indicates that 2014 and 2021/22 are most similar with a dissimilarity reading of 0.115. Despite of no ostrich in the lion diet during 2017 the diet of that year is considered closest to that of 2014 and 2021/22 with a dissimilarity value of 0.132. The dendrogram shows a more refined split of the years 2012 and 2020 that forms their own cluster (dissimilarity score = 0.15) that are the most dissimilar to all the other points and clusters, indicating the most even apportionment of prey during that time. The diet of 2013 and 2016 is considered the most different from the other years (0.2), presumably driven by the high contribution of kudu, red hartebeest, and gemsbok. Then, 2010/11 and 2019 are clustered together with a dissimilarity score of 0.216, and are likely associated with the higher zebra consumption in those years. The grouping formed by the years 2017, 2014 and 2021/22 is closely associated with 2015 and 2018 and was the next least dissimilar (0.241). The subsequent cluster of 2017, 2014, 2021/22, 2015 and 2018 is then the next most similar together with 2010/11 and 2019, with a score of 0.318. Then, 2013 and 2016 joined with a dissimilarity score of 0.349, followed by the 2012 and 2020 cluster joins all the other clusters created a dissimilarity score of 0.427.

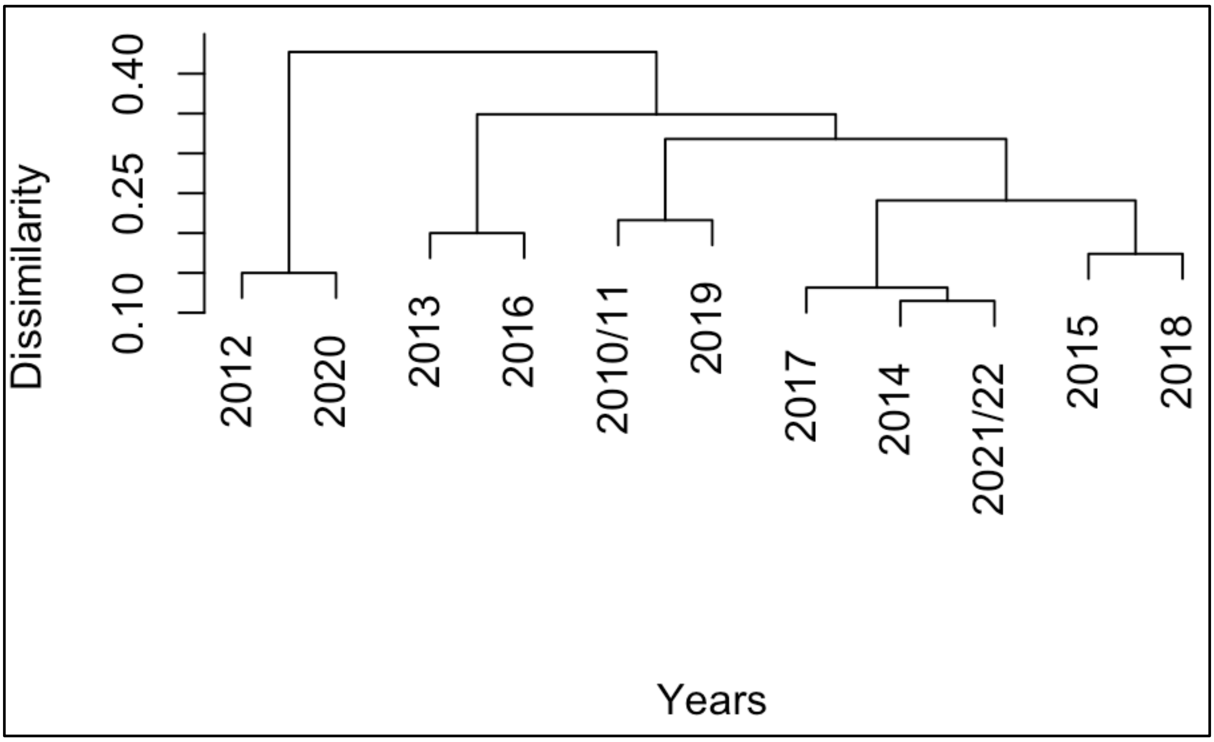

Figure 3.6 A dendrogram displaying the similarities or lack thereof in the large prey species composition consumed by lion each year for the time period between 2010 and 2022. The y-axis shows the degree of dissimilarity between the data from different years and the x-axis has the years labelled.

Variation in large prey biomass consumption over time

Seven out of the ten years, from 2011 to 2021, eland were the most significant contributor to large prey biomass consumption annually (Fig. 3.7). Gemsbok were, overall, the second greatest contributor to biomass consumption annually, with gemsbok actually the greatest contributor to biomass consumption for three of the years (2010/11, 2019 and 2020). However, since 2020, gemsbok was the third and fourth most significant contributor to biomass consumption. Generally, over the twelve-year history, zebra and ostrich contributed the least to the biomass consumption. An exception to that, was in 2011 where zebra contributed second most to the diet after gemsbok. Furthermore, kudu generally contributed the third most to the biomass consumed annually, but in 2013 was the greatest contributor by a large margin.

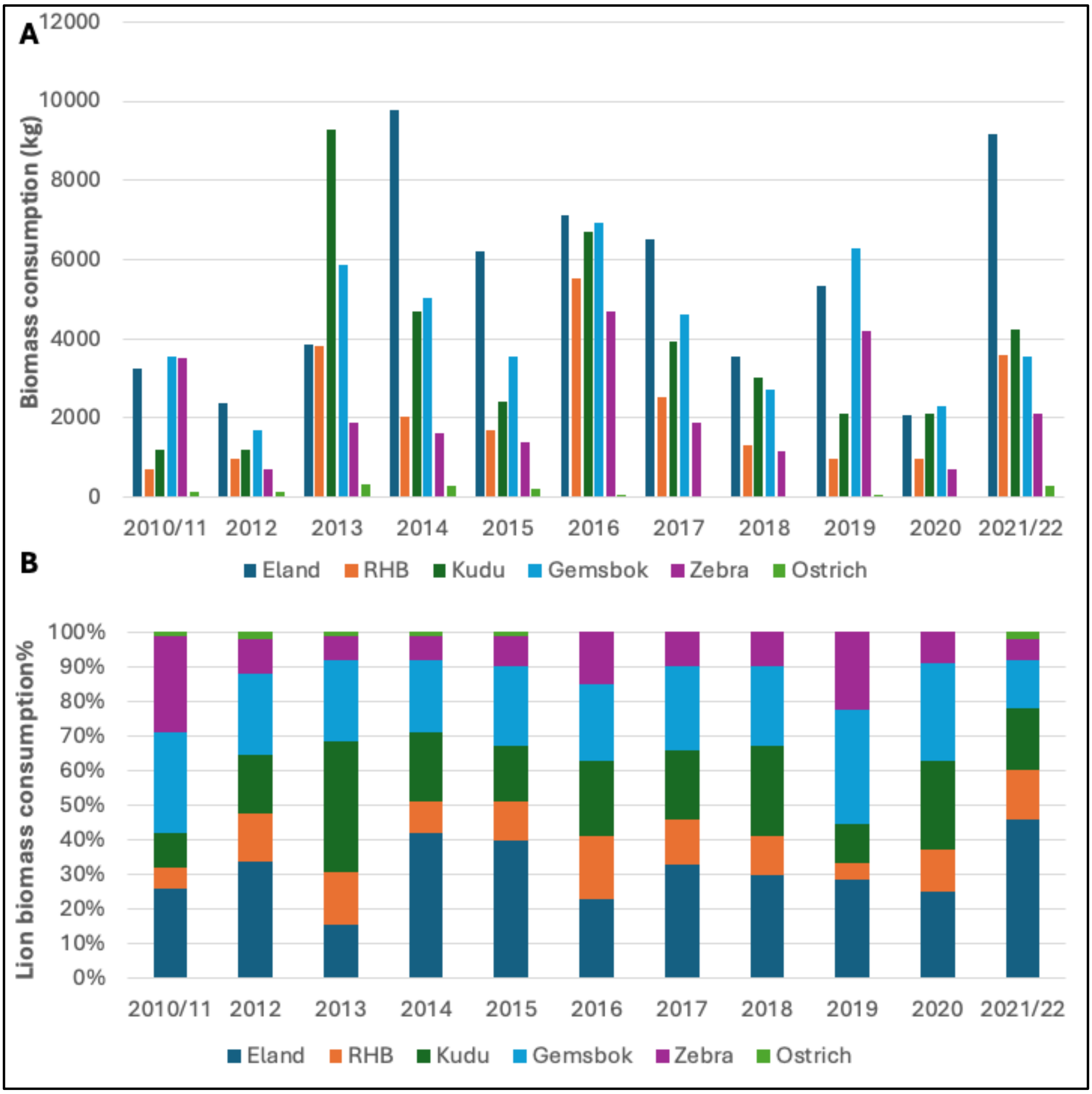

Figure 3.7 Large prey biomass consumption by lion from 2010 till 2022 as calculated from the recorded lion kill data. **(A)** Total biomass of the six large prey species (>50kg) consumed **(B)** Proportional biomass consumption

of the six large main prey species. *The 2010 and 2011 kill data were merged as too few kill sites were visited in 2010 soon after the lion reintroduction, and the kill data of 2021 and 2022 were pooled as kill data was only collected for the first 5 months of 2022.

Variation in prey abundance over time

The proportional large prey availability as calculated from the annual aerial census numbers has, over time, largely remained consistent (Fig. 3.6, also see Appendix D). However, the total numbers of large prey have dropped significantly since 2013 which was the year of highest availability, with 7 820 individual large prey animals recorded. This number dropped to almost half that number in 2021 with only 3 731 individual large prey animals recorded. Gemsbok is the most abundant species within KrNP and the population numbers of this species reached a peak of 2 582 in 2013 and then drastically declined to 843 individuals in 2021. Red hartebeest is the second most abundant species which also reached a peak in numbers in 2013 with 1 863 individuals counted and then dropping to a low of 840 in 2021. Over time, zebra were generally the third most abundant species and remained the most constant in numbers of between 1 088 and 805 individuals. Only in 2010 and 2011 were the numbers below 800. Eland steadily increased from 333 in 2010, to 1 116 in 2018 and then showed a significant decline to 516 individuals three years later. Kudu numbers fluctuated between 500 and 900 individuals during the 2010 – 2018 time period and only after that did it drop below the 500 individual mark, with 414 the lowest number in 2021. Ostrich increased up until 2013, with 1 109 birds, and then declined steadily to 313 individuals.

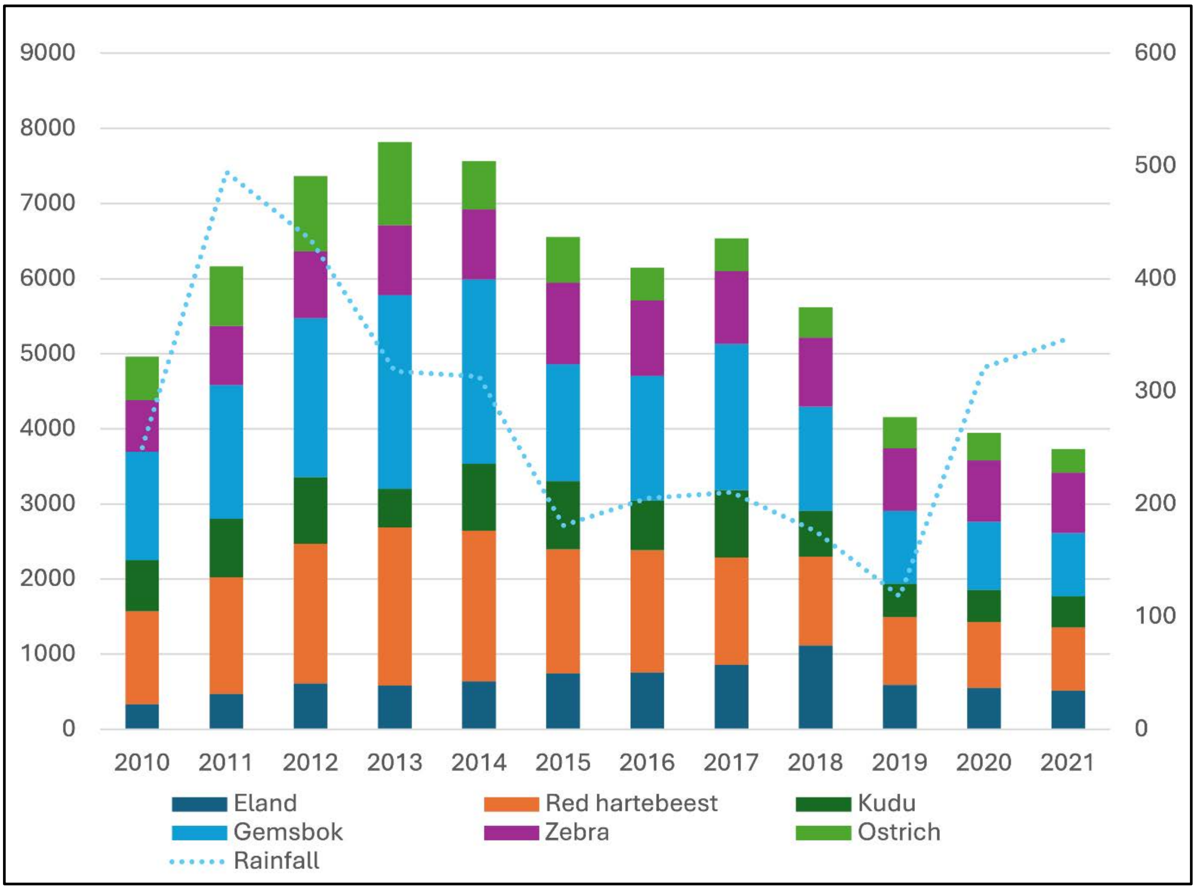

Figure 3.8 Annual aerial census numbers of the six large species (>50kg) that contribute to lion diet from 2010 till 2022, in the Karoo National Park. The rainfall recorded at the main camp over the same period is also displayed. *The 2011 count has been considered erroneous by park authorities and was replaced by the average count value calculated from the 2010 and 2012 numbers of each species. In the COVID year of 2020 no count was conducted and values portrayed are the average between the 2019 and 2021 count values for each species.

Prey preference variation over time as defined by the Jacobs Index

Over the 12-year period from 2010 to 2022, the overall prey preference trend indicates that kudu and eland were the most preferred prey (Fig. 3.9). Kudu were the most preferred prey and were utilised as such every year except during 2010/11 when it was preyed upon in proportion to its availability and in 2019 when gemsbok was marginally more preferred. Eland was favoured in seven of the 11 years and were preyed upon relative to the amount they were available during four years. Zebra was a preferred prey species only in the year immediately following the lion introduction in in 2010/11, otherwise zebra was not preferred, except when it was killed relative to its abundance in 2019. Gemsbok were preferred once in 2019, and was not favoured in four of the years (2013, 2014, 2016 and 2021/22). Ostrich were the least preferred species over the entire time period. Red hartebeest was largely preyed upon in relation to its availability, except during 2010/11, 2014, 2015 and 2019 when they were not preferred.

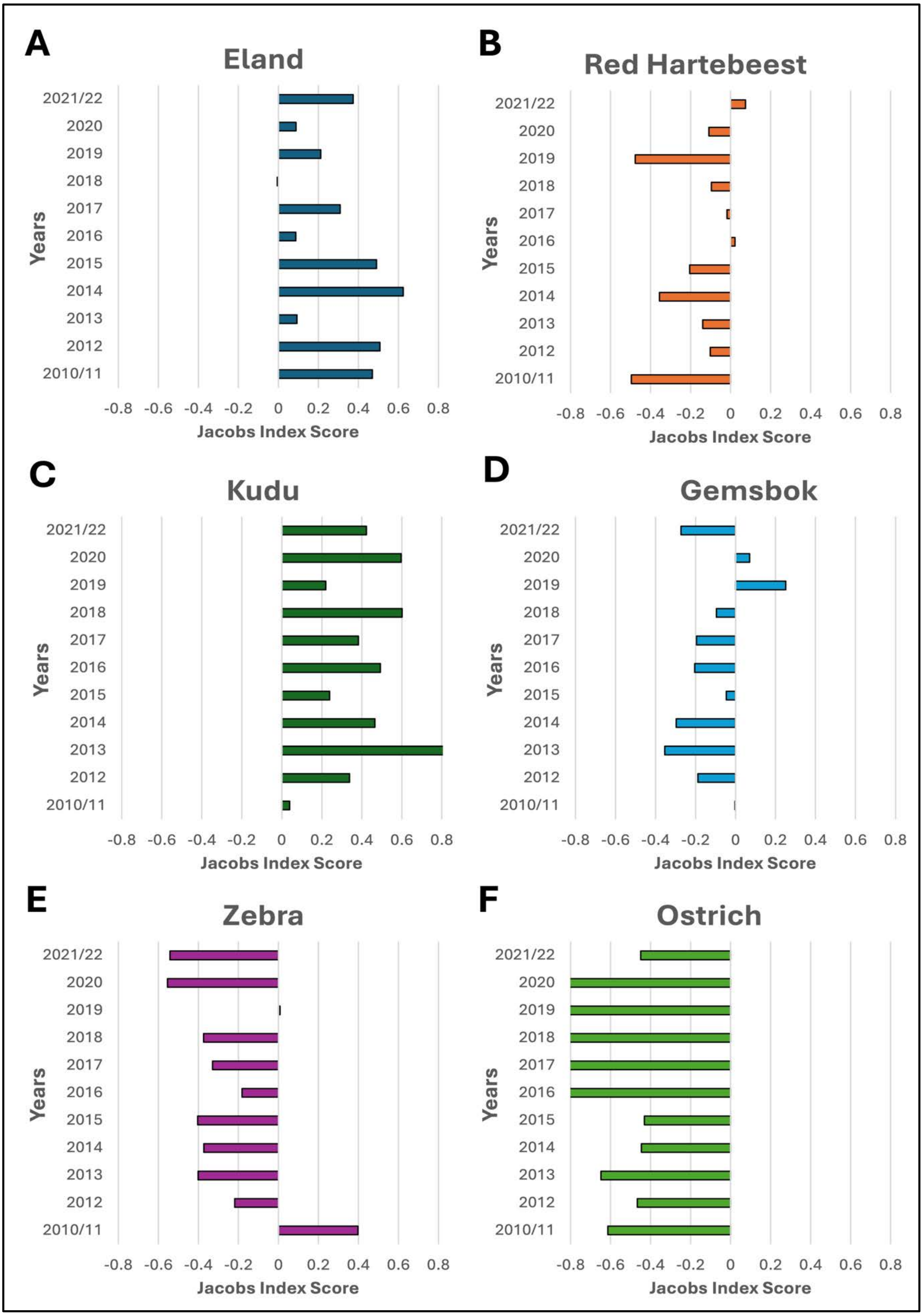

Figure 3.9 The Jacobs index scores for the six large prey species killed by lions from 2010 till 2022 - Eland **(A)**, Red Hartebeest **(B)**, Kudu **(C)**, Gemsbok **(D)**, zebra **(E)** and Ostrich **(F)**. *The 2010 and 2011 kill data were merged as too few kill sites were visited in 2010 soon after the lion reintroduction, and the kill data of 2021 and 2022 were pooled as kill data was only collected for the first 5 months of 2022.

From a biomass perspective, the overall trend showed that kudu was the most preferred biomass consumed, with eland biomass the second most preferred (Fig. 3.10). A noticeable difference was that the gemsbok and kudu were a slightly less preferred food item from a biomass perspective than every year in comparison to the actual number consumed.

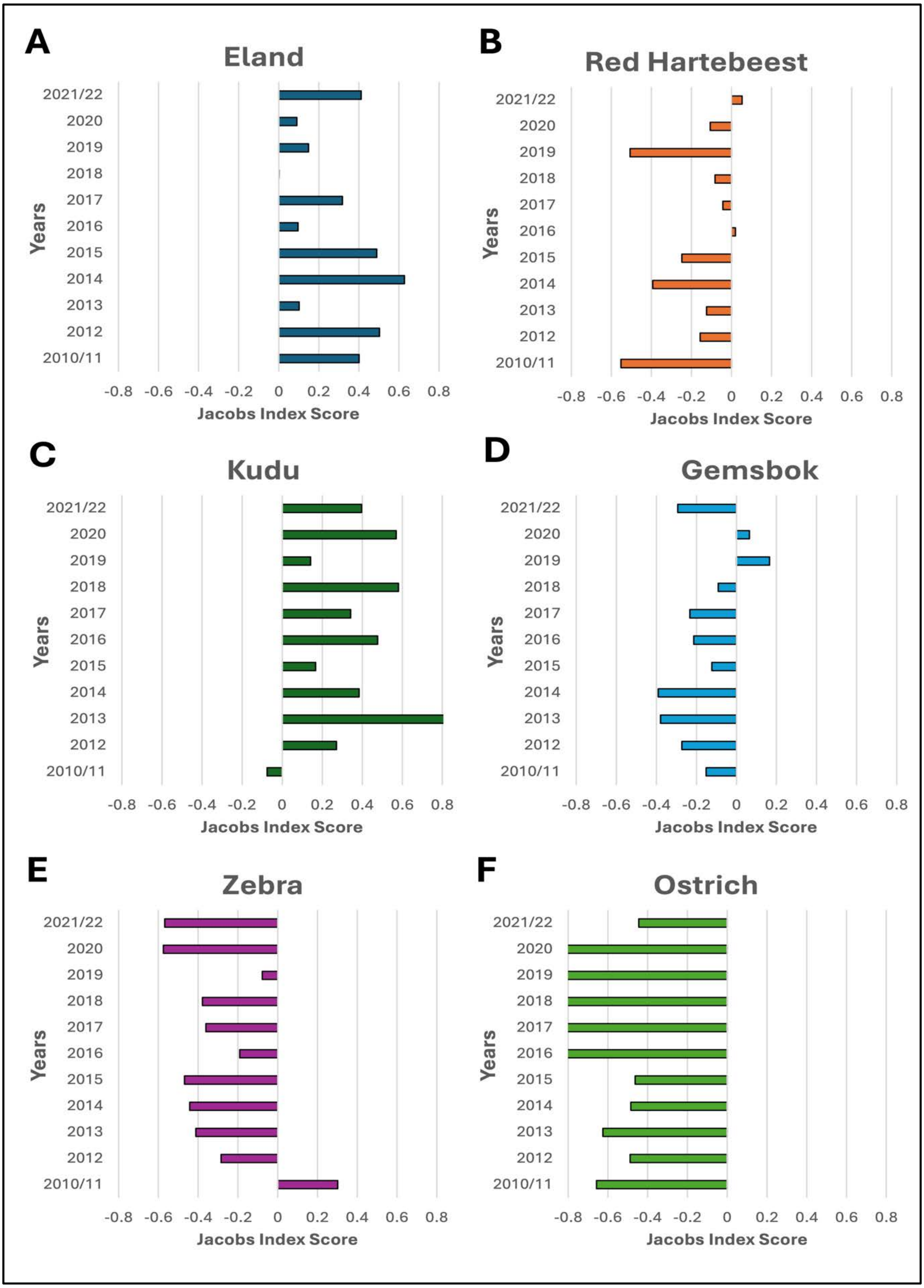

Figure 3.10 The Jacobs index values for lion food preference from a biomass perspective for the time period between 2010 to 2022 - Eland (A), Red Hartebeest (B), Kudu (C), Gemsbok (D), zebra (E) and Ostrich (F). * The 2010 and 2011 kill data were merged as too few kill sites were visited in 2010 soon after the lion reintroduction, and the kill data of 2021 and 2022 were pooled as kill data was only collected for the first 5 months of 2022.

3.4 Discussion

Lion dietary profiles are critical in understanding predator ecology (Owen-Smith & Mills, 2008; Becker *et al.,* 2013), the influence the predators have upon the prey populations and the knock-on effects impacting other trophic levels, which in turn can assist management decisions (Radloff & du Toit, 2004; Hayward & Kerley, 2005; Owen-Smith & Mills, 2008). However, in arid environments, like the KrNP, natural resources are limited thus resulting in low densities of lions and their prey (Eloff, 1984; Mills, 2015, Beukes, 2017). This provides challenges to estimate lion diets.

The adequacy of the contemporary and historic data sets were measured using the Brillouin's index. The years 2012 and 2020 were considered inadequate samples sizes and the years of 2010/11 and 2018, should be consider carefully when making deductions (*Table 3.3*). However, the years where the acute change were largely adequate, expect the years 2010/11 where deductions taken from those years need to considered cautiously.

I found, through detailed and intensive investigation that the diet of lions during 2021 and 2022, comprised of six large vertebrate species (> 50 kgs) and this is supported by historic ranger reports covering the period from lion introduction in 2010. The recent diet analyses revealed that eland, kudu and red hartebeest were the most often fed upon and, interestingly, these three species were fed upon in similar quantities with eland at 21.5%, greater kudu at 19.4% and red hartebeest at 20.8%. That said, the Jacobs index indicate a vast difference in preference with kudu the most preferred (D=0.42), eland second (D=0.37), while red hartebeest were actually not preferred and fed upon in proportion to their availability (D=0.07).

The affinity for lions to favour large prey is well documented (Stander & Albon, 1993; Radloff & du Toit, 2004; Hayward & Kerley, 2005; Davidson *et al.,* 2013; Beukes, 2016). Generally, three to five large and medium-sized prey species contribute to the majority of a lion's diet (about 80%) (Wright, 1960; Kruuk & Turner, 1967; Schaller, 1972; Rudnai, 1974; van Meulen, 1976; Olivier, 2021). This study recorded that >80% of the detected and identified prey, and approximately 98% to the overall prey biomass predated on by lions, were of medium to large-sized species but GPS cluster analysis are known to have inherit bias towards large prey (Tambling *et al.*, 2012; Beukes, 2016) and, thus, cannot be considered a true reflection for smaller prey consumption.

Furthermore, lions are known to have a diverse diet taking a wide range of prey including small prey species such as steenbok, porcupine and springhare (Eloff, 1984; Stander & Albon, 1993; Bothma & Walker, 1999; Sinclair *et al.,* 2003; Stander, 2003; Roxburgh, 2008; Beukes, 2016). Generally, the smaller species do not contribute significantly to the prey biomass consumed and most likely act as important "top ups" between predation events of larger prey (Eloff, 1984; Hayward & Kerley, 2005).

Additionally, lion studies conducted in other arid regions, have recorded that significant contributions to the total diet are made up of small prey species (< 50kg, Stander, 1992b; Stander & Albon, 1993; Bothma & Walker, 1999; Davidson *et al.*, 2013; Barnardo *et al.*, 2020). However, knowing which large prey species are preferred and utilised is essential to maintain a sufficient prey base for lion populations as it supports the bulk of the biomass consumed (Hayward & Kerley, 2005; Owen-Smith & Mills, 2008).

Lion's preferred prey mass is between 92 – 632 kg (Clements *et al.,* 2014), with a mean around 350 kg (Hayward & Kerley, 2005). Few potential prey species in KrNP are equal or greater than 350 kg, eland being the only exception (Skinner & Chimimba, 2005; Spies, 2017a). In the arid Kalahari, Beukes *et al.,* (2017) found that collectively, gemsbok, wildebeest, hartebeest and eland contributed 92% of total biomass consumed and that less than 4% of the total biomass consumed by lions was small prey. Eland were the most preferred species in the Kalahari (Beukes, 2016) but, in the Karoo, kudu were the most preferred prey species. Eland was preferred for all the years but were highly sought after in 2014 and 2015. The historic data, showed that from 2010 to 2020 kudu contributed 27% and eland 19% to the overall large prey diet. However, the detailed interrogation of diet during 2021/22 found that eland made up 26% of the species consumed and 40% to the biomass intake, whereas 24% of the species consumed was kudu that contributed 19% to the biomass intake.

Kudu might be a preferred prey species because it restricts itself to dense areas (Hooimeijer *et al.,* 2005; Gray *et al.,* 2007) which in this open arid environment is scarce (Palmer & Fairall, 1988; Letsoalo *et al.,* 2023). The areas with greater woody component have reduced visibility and thus could be beneficial for the lions to hunt in, as they can conceal themselves and stalk easier to make a successful hunt (Van Orsdol, 1984; Elliot, 1977; Hopcraft *et al.,* 2005). Thus, it might just be easier to kill kudu because of a habit type preference and way lions hunt within this environment. This requires further investigation, part of which will be investigated in Chapter 4.

Interestingly, eland are generally, within Southern Africa, not considered a preferred prey species presumably due anti-predator benefits provided by scarcity (Hayward, 2011; Hayward & Kerley, 2005; Louw, 2012). However, in the Kalahari (Beukes *et al.,* 2017), Madikwe and Pilansberg (Louw, 2012) eland were a preferred prey species for lion. In this study, eland is also preferred but less so when compared to kudu and, considering 94% of their diet is browse material (Watson & Owen-Smith, 2000), they spend the majority of their time in areas with greater cover and thus better stalking potential for lions to successfully hunt (Van Orsdol, 1984; Elliot, 1977; Hopcraft *et al.,* 2005). Furthermore, eland are versatile in their habitat selection, and can inhabit mountainous areas (Skinner & Chimimba, 2005), like parts of the KrNP. Multiple studies have shown that landscape curvature can aid in a successful hunt (Van Orsdol, 1984; Elliot, 1977; Hopcraft *et al.,* 2005) and it can thus be expected that these mountainous landscapes could aid lions in prey capture due to the cover provided by the broken terrain and the difficulty of the terrain underfoot that might hinder the ability of ungulates to flee (Wheatley *et al.,* 2021).

Conversely, gemsbok and zebra are not favoured. Both gemsbok and zebra feed significantly more on grass than compared to kudu and eland (Grobler, 1983; Strauss, 2015; Cain *et al.,* 2017). In KrNP, the grass is largely associated with the Lower Plateau regions (Bezuidenhout, 2016). The lower plateau areas are more open with less woody and shrubby components, except the riverbeds which are generally narrow strips of riverine woodland (Bezuidenhout, 2016). The lack of cover could possibly be attributed to the non-preference of these species (Hopcraft *et al.,* 2005).

The non-preference of zebra, except in 2010/11, is different to many studies where zebra contribute between 4% and 19% towards the dietary composition, and in certain regions zebra are the greatest contributor to lion diet (even if at low percentages; Schaller, 1972; Sunquist & Sunquist 1989; Stander, 1992b; Funston *et al.*, 1998; Druce *et al.,* 2004; Hayward & Kerley, 2005; Davidson *et al.*, 2013; Barnardo *et al.*, 2020; Briers-louw; 2020; Hayward *et al.,* 2023). Lion diet generally is well understood and researched but in a semi-arid region, like the KrNP, limited studies have been conducted (Beukes, 2016). Interestingly, the few studies done in semi-arid regions where zebra were present, they do contribute to the overall lion diet (Berry, 1981; Stander, 1992b; Davidson *et al.,* 2013). According to Berry (1981), who used reserve mortality records, zebra contributed 55% to the diet in Etosha. However, also in Etosha, Stander (1992) found that zebra contributed only between 8 and 9% to the lion diet and were only the third greatest diet contributor. Davidson *et al.* (2013) in Hwange, found similar results with plains zebra being only the fourth greatest contributor to lion diet making up between 8 - 9% of the diet. Davidson *et al.* (2013) also noted that zebra were not preferred. Furthermore, the contemporary diet part of this study from 2021/22 arguably provides the most accurate data and similarly found that only 8% of the diet were comprised of zebra making it only the fifth greatest contributor to lion diet and was also not preferred. However, few studies have specifically assessed mountain zebra's contribution to lion diet in comparison to the multiple studies relating to plains zebra contribution (Hrabar & Kerley, 2013) and mountain zebra interaction with lion merits further investigation.

Interrogation of the lion dietary trends over time suggests that the only acute changes were seen in 2010/11, 2013 and 2019. In 2011 it can likely be attributed to the animals being newly introduced and they were still adapting to their new environment (Miller *et al.,* 2013). The preference profile for 2011 showed a selection for gemsbok and zebra, which changed dramatically one year later, and then a decade long preference remained thereafter for eland and kudu.

The initial focus on zebra and gemsbok after lion introduction late in 2010, and the avoidance of kudu may reflect the type of exploring and disruptions that can happen when lions encounter new environments (Miller *et al.,* 2013; Davies *et al.*, 2016). A year after their reintroduction lion preference towards kudu increased. Furthermore, another year later, in 2013, a significant preference was shown to kudu. This potentially supports an expectation that lions may make abnormal choices in response to disturbance and it could be that certain old habits returned where they switch back to kudu, a prey species they were used to from where they originated in Addo (Wentworth, 2012). Additionally, prey behaviour, to avoid predation, may change spatially and temporally in response to the increased predation pressure after reintroduction (Valeix *et al.,* 2009; Tambling *et al.,* 2015; Davies *et al.,* 2016). As a result of this increased predation pressure, kudu may have shifted to become more diurnally active (Tambling *et al.,* 2015) to avoid the nocturnal activity of lions (Skinner & Chimimba, 2005) or may have moved more cautiously through dense vegetation, that provides good cover for lions (Davies *et al.,* 2016). Thus, this fluctuation in diet in the first three years after reintroduction may have been as a result of the predator and prey behavior within this altered ecosystem.

In 2019, the diet profile was another outlier from the norm where lions suddenly showed a renewed interest in gemsbok and zebra In comparison to the rest of the years apart from 2010/2011 gemsbok and zebra were again more preferred in 2019, while kudu’s preference dropped. The acute prey switch, seen in 2019, was short and is believed to be linked to environmental conditions, similar to other cases like in the Kruger National Park (Maruping-Mzileni *et al.,* 2017) where the predator switches lasted for longer periods. That said, the drought in KrNP hit its peak in 2019 (Moeletsi *et al.,* 2022) and prey switching, as a result of less rainfall, has been documented (Mills *et al.*, 1995). Even though browsers, like kudu, may have a more diverse feeding niche (Owen-Smith, 1979; Hooimeijer *et al.,* 2005; Gray *et al.,* 2007) they are known to decline during periods of low rainfall or drought (Owen-Smith, 1990; Dunham, 1994). Eland can withstand drought conditions well (Okello *et al.,* 2015) but have also been recorded in the southern Kalahari to decline by 35% after drought (Knight, 1995). Gemsbok and zebra are grazers that prefer grass (Relton, 2015; Strauss, 2015; Boyers *et al.,* 2019; Boyers *et al.,* 2021; Potgieter & Kerley, 2022). In a semi-arid environment, like the KrNP, grasses are less abundant in years of drought (Chiyangwa, 2018; Conradie & Theron, 2019; Letsoalo *et al.,* 2023; Milton *et al.,* 2023) and sweet thorn (*Vachellia karroo*) trees, the dominant trees in the KrNP drainage lines (Bezuidenhout *et al.,* 2024), are drought resistant (Orwa et al, 2009; Dingaan & du Preez, 2018). Resultantly, due to the lack of food, it is believed that zebra and gemsbok would have been in poorer condition and, thus, easier prey.

The lions in KrNP have shown their capability to hunt and use at least three large herbivores with ease (kudu, eland and red hartebeest) with a preference for kudu and eland that predominantly browse

(Watson & Owen-smith, 2000; Gray *et al.,* 2007). The KrNP lions also showed that they can adapt and change, when required, and food abundance is thus not necessarily a constraint driving escapes from the park. However, the preference for kudu and eland might be due to these prey species tendency to occupy and feed in denser areas with more cover (Watson & Owen-smith, 2000; Hooimeijer *et al.,* 2005; Gray *et al.,* 2007; Okello *et al*., 2015; Bezuidenhout, 2016) that presumably makes it easier to stalk and capture them If so kudu and eland might be key for lion persistence and these two herbivore species numbers must be carefully monitored to ensure there is a sufficient supply of these preferred prey. The importance of lion hunting habitat, apart from prey abundance, is then also addressed in the next chapter where I investigate the availability vs. catchability of prey within the KrNP.

3.5 Conclusion

This study aimed to provide a comprehensive understanding of the feeding habits of lions in KrNP by estimating their recent diet and investigating whether their prey preference has shifted over the past 10 years since their reintroduction in 2010.

Through GPS cluster analysis, the lion’s diet of the large herbivores bigger than 50 kilograms, in KrNP, revealed that three species contributed the bulk of lion diet, which were eland, kudu and red hartebeest. Gemsbok was also an important contributor while little use are made of zebra and ostrich. Kudu and eland were preferred prey species, whereas red hartebeest was fed upon relative to its abundance. With reference to lion biomass intake, eland was the greatest contributor by a large margin, followed by kudu and then red hartebeest and gemsbok and, less so, zebra and ostrich.

The historic lion diet was further analysed, by comparing kill records and game census data from the last decade, to ascertain if these dietary patterns have remained consistent or changed over time. While the findings largely suggest a continuity in prey preferences, acute changes were identified in 2010/11, 2013 and 2019. The acute changes in 2010/2011 and 2013 were likely a result of adapting to their new environment after their reintroduction to a drier region with different prey species. The noticeable change in prey selection experienced in 2019 was likely a result of prey condition change in reaction to the drought that peaked in that year.

Lion scat analysis which is known to provide information on small prey species that GPS cluster analysis will likely miss (Floyd *et al.*, 1978, Beukes *et al.*, 2017), is recommended to compliment the results of this study and to identify if indeed small prey contribute significantly to the diet of lions in the KrNP, alike to that of other, especially arid, regions (Eloff, 1984; Stander & Albon, 1993; Bothma & Walker, 1999; Sinclair *et al.,* 2003; Stander, 2003; Roxburgh, 2008; Beukes, 2016).

It is important for reserve mangers to obtain an accurate understanding of prey preference, kill frequency, and if there are any long-term fluctuations in the diet by the large carnivore within their region or reserve (Mills & Shenk, 1992; Bothma & du Toit, 2010; Fuller & Sievert, 2001; Power, 2003; Hayward *et al.*, 2005). These insights are crucial for the KrNP park management & conservation efforts, ensuring that both predator and prey populations are sustainably managed. Sustainable predator and prey numbers will allow for the reserve to adequately achieve its conservation and social objectives, provide a good tourism product, potentially contribute to the lion metapopulation, maintain good stakeholder relations and allow for the development of more comprehensive present and future adaptive strategies.

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CHAPTER 4

ENVIRONMENTAL FEATURES OF LION KILL SITES IN KAROO NATIONAL PARK

4.1 Introduction

Commercial and subsistence hunting, habitat restriction and conflict with humans threatens lions in Central, Eastern and Western Africa (Tranquilli *et al.*, 2014; Bauer *et al.*, 2022). However, in southern Africa lions (*Panthera leo*) are persisting and increasing, despite being eradicated from most of their historical range by the 1900's (Nowell & Jackson 1996). In South Africa lion populations persisted in the more remote regions of South Africa, which subsequently became national parks - Kruger National Park (Ferreira & Funston 2010), the Kgalagadi Transfrontier Park (Castley *et al.*, 2002; Funston, 2011) and Greater Mapungubwe Transfrontier Conservation area (Miller *et al.*, 2013). Lastly, lions also now occur in a large number of small reserves (Miller *et al.*, 2013). Between 1958 and 2018, authorities re-introduced 748 lions into 59 different reserves throughout South Africa that complies with meta-population functioning (Miller *et al.*, 2013, Selier *et al.,* 2024).

The meta-population management framework accepts that dispersal between the various reserves and regions are necessary to mimic natural dispersal of lion (Olivier *et al.*, 2009). Translocations, that are guided by the social dynamics of lions (Ferreira & Hofmeyr, 2014) are considered as the best practice (Miller *et al.*, 2013). Resultantly, South Africa's meta-population in one of the largest lion conservation units in Africa (Selier *et al.*, 2024).

The Karoo National Park (KrNP) near Beaufort West, Western Cape (Spies, 2017a) is one of the reserves forming part of the lion meta population, but managing lions within this arid region has been challenging (Bissett *et al.*, 2021). Multiple lions have escaped from the reserve's fenced boundaries, some of which travelled over 300 km and took 22 days to recapture, increasing the human-wildlife conflict with the livestock farming communities and stakeholders bordering the park (Spies, 2017a; Spies, 2017b). Such events can jeopardise relationships with stakeholders and, ultimately, the conservation aspirations of the KrNP.

The KrNP is situated in the Nama karoo, a semi-arid region of South Africa (Rubin *et al.,* 2001; Mucina & Rutherford, 2006; Spies, 2017a). In such areas of low productivity where resources are distributed unevenly across the landscape (Eloff, 1984; Mills, 2015; Beukes, 2017), and finding prey can be challenging for lions affecting their overall fitness and survival (Owen-Smith *et al.*, 2005; Dickie & Parsons, 2012; Tarugara *et al.*, 2024). Although the lions of KrNP prey on a diverse profile of prey species (Chapter 3) finding these animals in habitat suitable for successful engagement and killing (Kittle *et al.*, 2022) must be challenging as much of the area is extremely open and lacking sufficient stalking cover. Multiple studies showed lions preferred bushed grasslands or areas with denser vegetation to hunt (Van Orsdol, 1984; Spong, 2002; Hebblewhite *et al.*, 2005; Hopcraft *et al.*, 2005; Riginos & Grace, 2008; Davidson *et al.*, 2012; Tambling *et al.*, 2012; Davies *et al.*, 2016) while fine scale topographical change was preferred by lions in the Serengeti (Hopcraft *et al.*, 2005; Kittle *et al.*, 2016). Furthermore, fine scale underfoot conditions can also have an influence on preferred kill sites (Wheatley *et al.*, 2021).

The KrNP encompasses a variety of habitats, including succulent thicket (in small portions), low shrubland, and open plains with very little plant cover (Mucina & Rutherford, 2006; Bezuidenhout, 2016; Spies, 2017a), which host a range of herbivorous species adapted to semi-arid environmental conditions (Bezuidenhout, 2016; Spies, 2017a). Understanding the landscape selection of lions can help authorities, that are managing lions, make informed reserve management decisions based on the lion ecology. How lions use a landscape is largely influenced by prey movement (Loveridge *et al.*, 2009; Hayward & Kerley, 2009; Mosser *et al.*, 2009) and prey movement is largely influenced by accessibility of quality forage (Winnie *et al.,* 2008, Chamaille-Jammes *et al.,* 2013; Burkepile *et al.*, 2013) and proximity to water (Redfern *et al.*, 2003; Valeix *et al.*, 2009). Within semi-arid conditions, high quality food is scarce and unevenly distributed (Eloff, 1984; Owen-Smith *et al.*, 2005; Dickie & Parsons, 2012; Mills, 2015, Beukes, 2017; Tarugara *et al.*, 2024). Thus, herbivores adapt their feeding behaviours and diet based on the distribution of resource availability and environmental conditions (Simpson & Raubenheimer, 2001) especially those species that are water dependent (de Boer *et al.*, 2010; Redfern *et al.,* 2003). Furthermore, lion home ranges and territory establishment are largely mediated by the abundance, dispersion and predictability of food resources (Loveridge *et al.*, 2009; Tuqa *et al.*, 2014; Mosser *et al.,* 2015). Resultantly, lion movements would be expected to be in the areas where prey are most abundant (Ogutu & Dublin, 2004; Tuqa *et al.*, 2014). Considering the variation in habitat across KrNP and the reaction of prey species to this heterogeneity lion kill sites are expected to be unevenly distributed across this area, with some landscapes having disproportionately more kill sites than others.

At a smaller scale when conducting a hunt, lions stalk their prey and thus require sufficient cover to make a successful kill (Hopcraft *et al.,* 2005; Loarie *et al.*, 2013; Davies *et al.*, 2016). Lions would typically have a strategy of stalking and hiding using available cover, followed by a short rush over relatively easy-going terrain (Schaller, 1972; Van Orsdol, 1984; Stander 1992; Davies *et al.*, 2016). Additionally, prey intentionally select areas that are more open with greater visibility as they feel safer (Scheel, 1993; Hopcraft *et al.,* 2005; Davies *et al.*, 2021). This dynamic predicts that within a specific landscape, lion kill sites will have denser vegetative cover providing concealment for the lion to successfully stalk, and possibly also terrain more difficult underfoot that will hinder prey to flee attack, irrespective of prey abundance. It could also be argued that the thick vegetation could aid prey escape as they may dive into the thick bush (Davies *et al.*, 2016)

Furthermore, within the KrNP, the lions roam freely across the 883 km^2 of the park but most of the reserve is comprised of open habitats, with little plant cover available, which is deemed suboptimal hunting habitat for lions (Hopcraft *et al.,* 2005; Loarie *et al.*, 2013; Davies *et al.*, 2016). Limited habitat available for successful hunting might have consequences for lion persistence across the entire landscape. The lions may be restricted to only a fraction of the total area of KrNP where they can successfully stalk prey, and such areas might not necessarily have the highest prey densities. This can compound the conflict between prides fighting for optimal foraging areas and, ultimately, the necessary resources required to survive. Furthermore, not all prey might thus be available as it might only be possible to kill animals in very specific areas. Understanding this prey catchability dynamic is key for the management of lions in this arid landscape, and within semi-arid environments generally (Tambling *et al.,* 2012).

In this chapter, I focus on improving the understanding of lion feeding habitats within the KrNP by assessing the distribution of lion kill sites across the four broad landscape types (considering slope, vegetation, and altitude) characteristic of the park and, on a finer scale, comparing specific terrain and vegetation characteristics at kill locations with non-kill site locations. It could be expected that the lions will prefer to hunt in areas that are more accessible/less mountainous (Carbone *et al.,* 2007; Wheatley *et al.*, 2021) and, on a finer scale have denser vegetation cover (Loarie *et al.*, 2013; Davies *et al.*, 2016). Lion might also select for more uneven terrain on a fine scale as it could cause fleeing prey to slip and hence improve chances of capture. Lion may also select areas that are less rocky in order to ensure they do not injure themselves during the hunt but, conversely, more rocky areas can also hinder prey escape (Wheatley *et al.*, 2021). Understanding where lions kill their prey in this arid environment should provide greater understanding of what drives lion movement and habitat preference within the Karoo landscape and, ultimately, provide a greater understanding on whether a lack in optimal hunting habitat could potentially drive lions to search for prey beyond the boundaries of the KrNP.

4.2 Methodology

4.2.1 Study Area

The study was conducted in the KrNP and focused on the eastern half of the reserve. The KrNP, found in the semi-arid Great Karoo, covers approximately 883 km^2 (Saayman *et al.*, 2009; Spies, 2017a) located between 32°10’S-32°23'S and 22°15'E-22°35'E (Fig. 2.1).

The KrNP area receives predominantly summer rainfall and has a mean annual rainfall that varies significantly throughout the park, ranging from 175 mm in the East, to 406 mm in the West. Most rain (60% – 75%) occurs in summer (Rubin *et al.*, 2001; Spies, 2017a). The KrNP experiences cold winters, with a mean minimum winter temperature of 3.5 °C, and hot summers, with a mean maximum summer temperature of over 32 °C.

The mountains within the park form part of the Great Escarpment which differ significantly in elevation from 820 – 1 620 masl (Spies, 2017a). The park's contrasting elevation has a marked influence on the climate, with a cool steppe climate associated with the Upper Plateau and the steep elevation, and precipitation gradient rapidly changing to a warm steppe climate in the eastern, southern and western lowland sections of the park (Spies, 2017a). Winter precipitation comprises largely of heavy frost and periodic snowfall atop the Nuweveld Mountains (Spies, 2017a). The vegetation growth season, during summer (September to May), lasts seven to eight months. The predominant westerly and north westerly winds have a scorching effect on the soil and vegetation (Spies, 2017a).

The park hosts an array of fauna, with 58 mammal species and over 200 bird species (Spies, 2017a). Mammal species include plains game typical of the Karoo landscape, such as (in order of abundance) gemsbok, red hartebeest, springbok, zebra, kudu, eland, ostriches and grey rhebok (Spies, 2017a).

The semi-arid KrNP comprises of two biomes namely Nama-Karoo, which covers the largest section of the park, and the Grassland biome that covers a relatively small section of the park at the top of the plateau in the north (Spies, 2017a). Within the reserve, 15 landscape units have been identified that can be further categorized into four broad landscape types, which are largely defined by the associated elevation and gradient (Bezuidenhout, 2016; Spies, 2017a). The four landscape types are: a) the Nuweveld mountain plateau and ridges (totalling 5% of the reserve) also referred to as upper plateau, b) terraces of the Nuweveld mountain mid-slopes and mid-plateau (20%) also referred to as middle plateau, c) valley bottomland also referred to as lower plateau (71%), and d) bottomland drainage line woodland (4%), see Table 4.1 for a detailed description of each landscape types characteristics and composition.

Table 4.1 *A description of the four broad landscape types of the Karoo National Park with the vegetation units each landscape comprises of listed (adapted from Bezuidenhout, 2016).*

Upper Plateau (Nuweveld Mountain plateau and ridges)	*Montane Grassland*	High altitude, generally with a gentle gradient. Area covered by grasslands with sparsely scattered shrubs/fynbos. Shrubs vary between dwarf shrubs, more montane shrubland (often < 1 m high), fairly dense perennial shrub patches localised to depressions and shallow valleys, and semi-woody shrubland that occurs on the steep higher midslopes directly below the escarpment.
	Leegtes / wetlands	
	Shrub thicket	
	Mountain Shrubland	
	Short Shrubland	
Middle Plateau (Terraces of the Nuweveld Mountain midslopes and mid-plateau)	*Grewia robusta* Shrubland	Medium altitude, generally steep gradient, with some level "shelfs". The steep, unstable to stable midslopes and foothills are covered by Karoo grassy dwarf shrublands. The flat middle escarpment has a high, often large (over 1 metre high), shrub and grass component.
	Grassland	
	Karroid Grassland	
	Searsia sparse Shrubland	
Lower Plateau (Valley bottomland)	Bossieveld	Low altitude, generally gentle gradient, in places flat. Characterised by Karoo succulent dwarf shrublands that occur on the foothills and on the lower more arid and degraded rocky footslopes. Low shrubland, occur in flat, low-elevation floodplain areas and the aridity increase further away from the escarpment edge.
	Sparse Bossieveld	
	Salsola veld	
	Leegtes / Depressions / wetlands	
	Thornveld	
Drainage Line Woodland	Woodland	Largely at lower altitude, but there are patches in the middle and upper plateau. Generally gentle gradient with steeper sections nearer to the slopes. It comprises of Riparian Woodland, closely associated with the major drainage lines or rivers. This landscape unit is often the only densely vegetated woodland.

The study area (Fig 4.1), totalling 463 km^2, covered 53% of the total KrNP (Fig. 2.1) and comprised of 45% of the available lower plateau (known as valley bottomland in Bezuidenhout, 2016), 67% of the middle plateau, 100% of the upper plateau and 64% of the drainage line woodland landscape types (Table 4.1). The study area was restricted to the eastern portion of the park due to accessibility and logistical constraints, but it provides a representative sample of the reserve and its four broad landscape types.

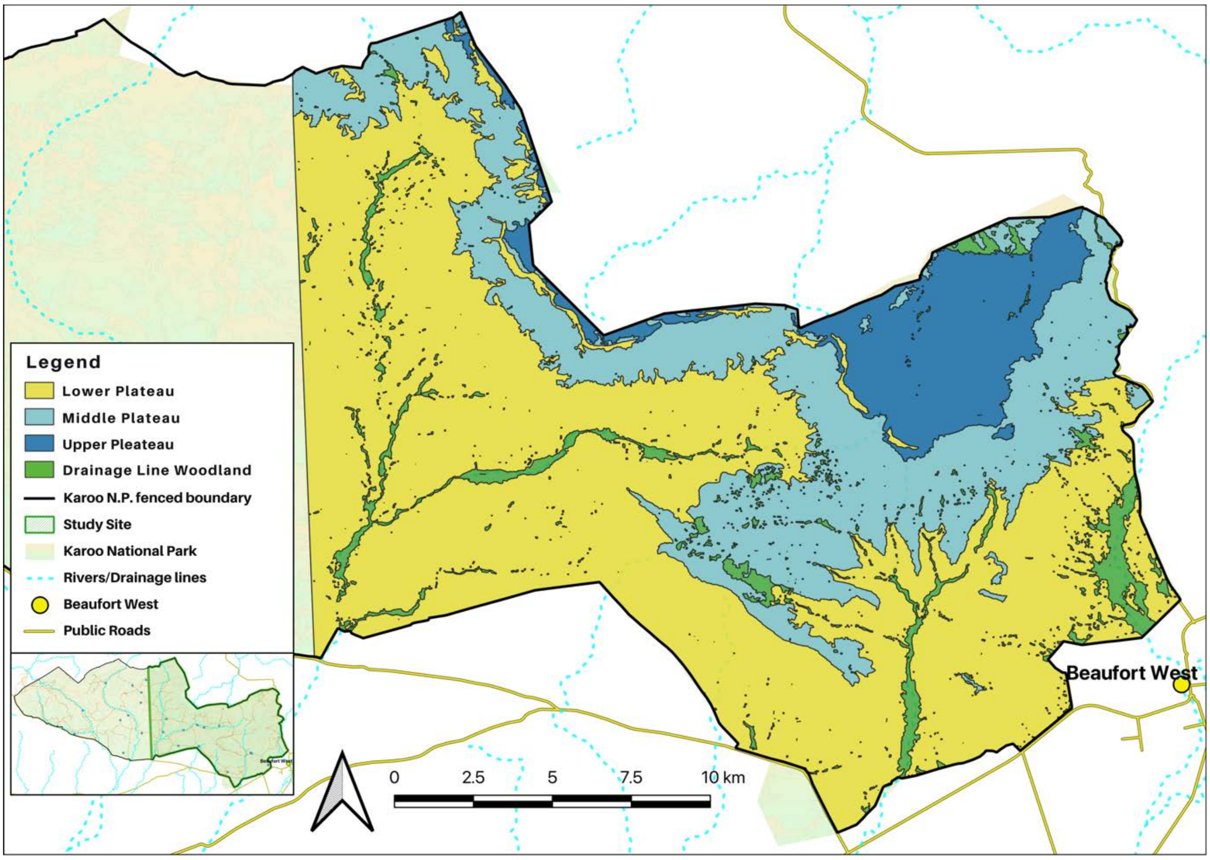

Figure 4.1 The location of the study area within the Karoo National Park's (inset), with the distribution of the four major landscape units– lower plateau, middle plateau, upper plateau and drainage line woodland - shown (QGIS Development Team, 2021).

A more comprehensive account of the biotic and abiotic features of the KrNP and study area have been described in Chapter 2.

4.2.2 Data Collection

Lion kill sites were identified over a 15 month period between April 2021 and May 2022 using GPS cluster analysis of lion location points obtained from eight lions fitted with VHF and IR-SAT collars. The kill sites were identified, visited and their key habitat features measured in the field. To establish if the kill sites differ from other locations within the KrNP environment a subset of randomized control sites were identified and measured. The characteristics of the kill and control sites were then compared and tested for significant differences.

4.2.2.1 Kill site identification

The collared lions provided a representative sample (at least one collar per pride) of the lion prides present within the park at the time of study (Table 4.2), with only two lionesses not associated with prides unaccounted for. A detailed description of how the kill sites were identified and recorded is in chapter 3.2.4.

Importantly, the data collected needed to be comprehensive and representative of the entire study site in order to accurately analyse kill site location preference over the landscape. Potential kill site clusters and consequent locations were thus extracted from the location data in an objective, robust and unbias manner following a rigorous protocol.

With the logistical and timeous constraints and not being able to visit every cluster formed, the clusters for investigation were prioritized based on the following criteria; the ratio comparison of distance moved 24 hours before and after the cluster formation (called R24 - with a higher ratio indicating a higher likelihood of a kill), clusters where lions had remained at the location for a longer period of time and clusters that start during the night due to lions hunting more at night (Tambling et al. 2012).

For this study, cluster investigation was prioritized for clusters that were predicted to be a kill site. We categorized the clusters into “likely clusters” (where we were more confident) and “potential clusters” (where we were less confident). A “Potential cluster” was defined as a cluster that had a R24 ratio of ≥ 3 and duration time ≥ 8 hours and being formed during the night. A “Likely cluster” was considered as a cluster that had a R24 ≥ 10 and duration time ≥ 12 hours and being formed during the night. A “Potential cluster” was defined as a cluster that had a R24 ratio of ≥ 3 and duration time ≥ 8 hours and being formed during the night. A “Likely cluster” was considered as a cluster that had a R24 ≥ 10 and duration time ≥ 12 hours and being formed during the night. The majority of the likely and potential clusters were visited and the clusters that occurred outside of these parameters were largely excluded from investigations unless either the R24 or duration stats alone suggested a likely kill site (Fig. 3.2).

The first GPS location point of an identified cluster was loaded onto a handheld GPS unit and was used as the start point to search for prey remains. The clusters points were visited on an average of 33.5 days (range 1-126 days) after the cluster formation with 56% visited within 30 days of formation. The GPS cluster point was deemed worth visiting if they were more recent than 60 days. Cluster locations were tracked to by road, as far as possible, and then by foot. The area around the identified location point of a cluster was extensively searched, irrespective of time taken, within a 100 m radius, for evidence of prey remains (Tambling *et al.,* 2012; Sand *et al.,* 2005) and this was generally done using a spiral walking pattern.

Table 4.2 *The known individual lions, and their general group structure within the Karoo National Park, during the study period March 2021 – May 2022. The sex and collar status for the study period are presented with collar period broken into months, with dark grey blocks indicating periods when data was reliable for the entire month, and the lighter grey blocks indicate the data that was reliable/usable for only some of the month. Note, the groupings/prides varied over the study period, but these were the general social dynamics.*

Groups	LION	Sex	Collar Period Jan 2021 - May 2022																
			J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
BF - Natie	B-Female	F	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Natie	F	■	■	■	■	■	■	■	■	▨								
Inge & D.	Inge	F	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Inge Daughter	F	■	■	■	■	■	■	■	▨									
"The boys"	Nkululeko	M	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Tuba	M	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
"The surprise 3"	MV/Nomonde	F					▨	▨	■	■	■	■	■	■	■	■	■	■	▨
	Renata	F									▨	■	■	■	■	■	■	■	■
	Plus 1	F	N/A																
Solo	Rietvallei	F	N/A																
Solo	D-Female	F	N/A																

4.2.2.2 Non-kill site/control site selection

We initially considered using clusters that yielded no signs of kills as control sites but when the success rate of finding kills greatly surpassed the failures we decided, after three months, to use a pairwise approach and used those pair wise plots for comparison. These paired non-kill/control sites were selected to be in a random direction 300 m away from the actual kill site. The selected 300 m distance was a trade-off between a distance considered far enough from a kill site to capture fine scale habitat differences, but still close enough to make the sampling effort logistically feasible considering the often very inaccessible mountainous terrain and time constraints of the study. The same terrain and vegetation feature measurements were taken at both the kill and control sites.

4.2.2.3 Terrain and vegetation feature measurements

At each site where evidence of a kill was found, the kill site characteristics were measured from the location where the greatest quantity of stomach content was found. Lions often remove the digestive organs and its associate content before dragging carcasses to a more suitable feeding spot and hence the location where the stomach content of partially digested plant matter were located were considered the closest point to the actual kill site (Schaller, 1972; Tambling *et al.,* 2010; Loarie *et al.,* 2013). In the few instances where no stomach contents were found, the location where the most prominent evidence of the kill was found was considered the kill site. At each identified kill and non-kill site the visibility, vegetation cover, vegetation height, terrain rockiness and fine-scale prey availability were measured.

Visibility measurements

A rangefinder (Bushnell, Kansas, USA) and/or tape measure was used to take visibility measurements in the four cardinal and four intercardinal directions (i.e. N, NE, E, SE, S, SW, W, NW). These visibility measurements were made at two heights above ground level, the first at 0.4 m that is believed to be the minimum height of cover needed by lion for stalking (Elliot *et al.*, 1977), and then at 1.5 m that is considered the average eye height of kudu & zebra (Davies *et al.*, 2021). The visibility measurements at 1.5 m were taken by placing the rangefinder on the top of a pre-marked collapsible hiking pole while the 0.4 m measurements were taken from a 0.4 m heigh wooden stake specifically cut for this purpose. While holding the rangefinder at a height of 0.4 or 1.5 m parallel to the surrounding slope the distance to the nearest obstacle (boulder, shrub, tree and occasionally ridge line) breaking the field of vision in each of the eight directions were measured. Resultantly, there were eight visibility measurements at 0.4 m and eight measurements at 1.5 m, every 45^{o} around the kill/non-kill site. The average and minimum visibility at the respective heights were then calculated for each kill and control site and used for comparative purposes (Riginos & Grace, 2008). By using the minimum visibility distance analysis at each site, it eliminates the outlier measurements where the visibility exceeded 100's of meters.

Grass and shrub cover and height estimates

In addition to the line-of-sight visibility measurements, we also measured the height and cover of both grass and shrubs. The cover and general height of the grass and shrubs layer surrounding the centre of a kill and control site were estimated within a 5 m and 15 m radius respectively. Grass and shrubs were pooled in both the general height and cover estimates and woody plants under 1.5 m tall was considered a shrub. The percentage grass and shrub cover within each circle (5 & 15 m radius) around the kill site and control site centre was visually estimated and reported to the nearest 5% increment. The typical grass and shrub height within each of the circles was visually estimated and expressed according to a seven-point score as indicated in Table 4.3.

Table 4.3 Grass and shrub height scoring criteria.

Score	*1*	*2*	*3*	*4*	*5*	*6*	*7*
Criteria	*0 – 10cm tall*	*10 - 30cm tall*	*31 - 50cm tall*	*51 - 70cm tall*	*71 - 100cm tall*	*101 - 120cm tall*	*121 - 150cm tall*

Tree cover and density

Tree cover and density around the kill/non-kill sites were also estimated and reported within a 5 m and 15 m radius from the actual kill and control site centre. Woody plants over 1.5 m tall was considered a tree. The percentage of the surface area within each circle around the kill site covered by trees was visually estimated and reported to the nearest 5% increment. The density of trees was also visually estimated and reported using a five-point scale (Table 4.4).

Table 4.4 *Tree density scoring criteria.*

Score	**1**	**2**	**3**	**4**	**5**
Criteria	No trees	low tree density (stems ±10m apart)	Moderate tree density (5-10m apart)	High tree density (2-5m apart)	Impenetrable tree density (<2m apart)

Terrain rockiness

The nature of the terrain across the KrNP varies dramatically with regards to the abundance of loose surface rocks varying from fist to soccer ball size, and it was considered an additional variable that might affect the catchability of prey (Gaynor *et al.*, 2019; Wheatley *et al.*, 2021). Again, the estimate was made and reported within a 5 m and 15 m radius around each kill and control site. The percentage loose rock cover was not only visually estimated and reported to the nearest 5%, but also categorised according to a five-point scale (Table 4.5).

Table 4.5 *Terrain rockiness point scoring criteria*

Score	***1***	***2***	***3***	***4***	***5***
Criteria	*No rocks - no obvious rocks, no real obstruction*	*Partially clear - Can Walk without needing to focus on where to step, not many rock obstructions*	*Mildly rocky - Need to take note of rocks as you step but little issue of finding a place to put your foot*	*Rocky - Need to focus on where you step and with little space to put your foot on an open surface*	*Very rocky - Cannot step without stepping on a rock*

4.2.2.4 Fine-scale prey availability

At each kill and control site an indirect measure of prey availability was made using dung transects (Barnes, 2001). At each site a 60 m transect was walked into each of the four cardinal directions. Along each 60 m transect line the number of independent dung piles within one metre from either side of the line was categorised and counted resulting in a survey area of 120 m^2 per transect line and 480 m^2 per kill and control site.

Dung was characterised according to both age, size and shape. Since several prey species have dung pellets very similar in size and shape a cautious approach was taken to group the dung into five easily identifiable size and shape categories which in turn can be attributed to specific species or groups of species (Table 4.6).

Table 4.6 *Herbivore dung count categories*

Category	**Medium**	**Large**	**Mega**	**Zebra**	**Ostrich**
Species	Springbok, Duiker, Grey Rhebok	Kudu, Red hartebeest, Gemsbok	Eland	Cape mountain zebra and Plains zebra	Ostrich

The dung was further assigned to four age categories (Table 4.7) and dung from categories 1, 2 and 3 were considered and tallied in these surveys, narrowing the window of prey availability down to within a couple of months (varies based on the time of the year) before or after a kill was made (Ahrestani *et al.*, 2018).

Table 4.7. *Herbivore dung age categories*

Category	***1***	***2***	***3***	***4 – N/A***
Species	*Fresh and wet with odor*	*Outside is dry but still intact has a darker colour and smooth or with small hairline cracks*	*Outside is dry, slightly faded but still largely intact*	*Colour of pellets faded or cracks very prominent– considered too old and not recorded*

4.2.3 Data analysis

4.2.3.1 Landscape preference

The location of kill sites in relation to the broader landscape types were assessed to identify if there was any hunting preference, or avoidance, for a specific broad landscape type within KrNP. Each kill site location was georeferenced and allocated to a specific landscape type by plotting the kill site location onto a map showing the area covered by each landscape type – figure 4.1 using QGIS version 3.26.2-Buenos Aires (QGIS Development Team, 2021).

Landscape preference was calculated according to the Jacobs' index (*D*) (Jacobs, 1974) using the following equation:

$$D = \frac{r-p}{r+p-2rp} \tag{1}$$

where *r* is the proportional contribution of lion kills in the broad landscape type and *p* is the proportional surface area availability of that specific landscape type. The lion kill data obtained using GPS cluster analysis provided *r*, while *p* was obtained from Bezuidenhout (2016) and adapted/clipped to study site using QGIS.

The Jacobs index allows for evaluating hunting landscape selection when different relative portions of landscape are compared (Jacobs, 1974). The resulting value scores between +1 and -1, with zero indicating no selection, +1 indicating maximum preference, and -1 indicating maximum avoidance (Jacobs, 1974). Furthermore, a value between -0.2 and 0.2 indicates that the landscape type was used as would be expected and in proportion to relative availability (Hayward *et al.,* 2011; Beukes, 2016).

4.2.3.2 Vegetation, terrain and prey availability comparisons

To determine if identified kill site cluster characteristics differed significantly from their immediate surroundings comparative 'paired' control sites were sampled. After testing for data normality and homoscedasticity, all site characteristic data (i.e., for both control and kill sites) conformed to parametric assumptions and no further transformations were required. Control and kill site characteristics (i.e., visibility, vegetative cover/density, terrain rockiness and surrounding prey availability) were then compared using paired two-sample t-tests (Al-Kassab & Majeed, 2022) for means implemented and visualised in GraphPad Prism v10.3.1 (GraphPad Software, CA, USA; www.graphpad.com).

4.3 Results

4.3.1 Kill Sites

During the 15-month study period 2 945 clusters were identified. 358 of these clusters were identified as potential kill sites and, of those, 171 were highly likely kill sites (Table 4.8). Effort was made to visit all the highly likely kill sites created during the 15-months and only 9 (5%) of the 171 highly likely clusters were not visited. Of the 162 highly likely clusters visited 119 yielded results - 97 could be confirmed as kill sites and 22 were recorded as non-kill or resting sites The remaining 25% (*n*=43) were found to be "duplicates" where two or more lions created GPS clusters within the same area. These "duplicate clusters" were therefore discounted. Additionally, 65 "potential clusters", that displayed statistics that indicated a decent possibility of a kill (either the R24 or the duration displayed a high likely score), were investigated and 47 recorded kill sites. Resultantly, 227 total sites were visited and measured during the study (Fig. 4.2) with 144 recorded kill sites, of which 37 kill sites were measured without a control site and 107 kill sites were measured with the associated control site. The efforts in the field work were extensive, objective and is considered representative of lion large prey kill sites within KrNP.

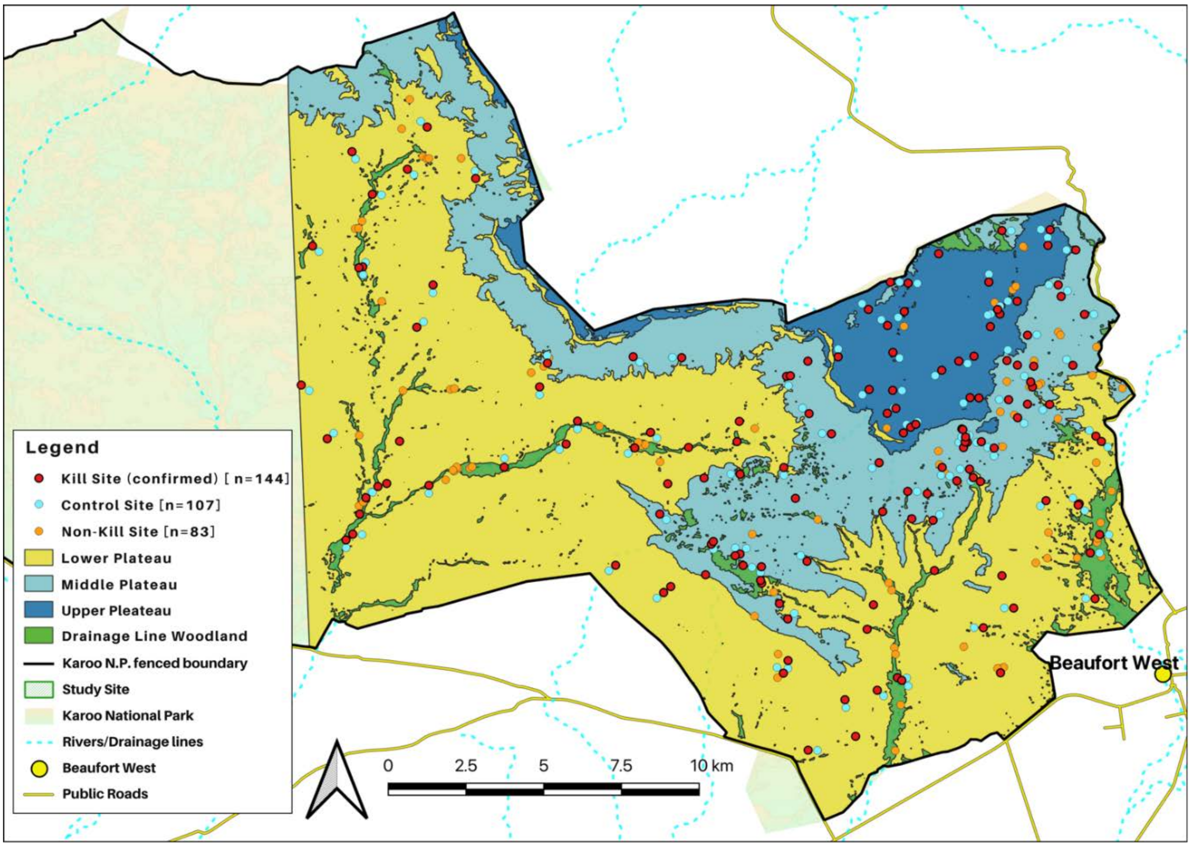

Figure 4.2 The distribution of kill sites (red dots), non-kill cluster sites (orange dots) and the control sites (light blue dots) across the four broad landscape types, visited during the study period from March 2021 and May 2022 in the Karoo National Park. (QGIS Development Team, 2021).

The study site of 463 km^2, had a proportional makeup of 61% lower plateau, 25% middle plateau, 9% upper plateau and 5% drainage line Woodland (Table 4.8). During the study period, 45 kills were located in the lower plateau, 44 in the middle plateau, 26 in the upper plateau and 29 in the drainage line woodland.

Table 4.8. *The four broad landscape types and their characteristics – area (km2) and the proportional percentage coverage of the study site (in brackets), the total number of clusters, number of potential clusters formed, number of likely clusters formed, number of potential clusters visited and the proportional percentage visited (in brackets), number of likely clusters visited and the proportional percentage visited (in brackets) and the total number of kills recorded in each of the four broad landscape types.*

	Area (km^2) (Proportional study site coverage percentage)	Total clusters	Total potential clusters	Total likely clusters	Potential clusters visited (Proportional percentage)	Likely clusters visited (Proportional percentage)	Kills
Lower plateau	281.2 (61%)	1034	117	56	74 (63%)	55 (98%)	45
Middle plateau	115.7 (25%)	685	113	60	63 (55%)	56 (93%)	44
Upper plateau	43.8 (9%)	513	35	16	32 (91%)	16 (100%)	26
Drainage line woodland	22.5 (5%)	713	93	39	58 (62%)	35 (90%)	29
Total	463.15	2945	358	171	227 (63%)	162 (95%)	144

4.3.2 Landscape preference

Drainage line woodland was highly preferred as kill sites with a Jacobs index value of 0.73 (Fig 4.5). The second most preferred landscape was the Upper Plateau with a 0.49 Jacobs index value followed by the middle plateau with a score of 0.3. Non-preference is shown for the lower plateau area with a score of - 0.55.

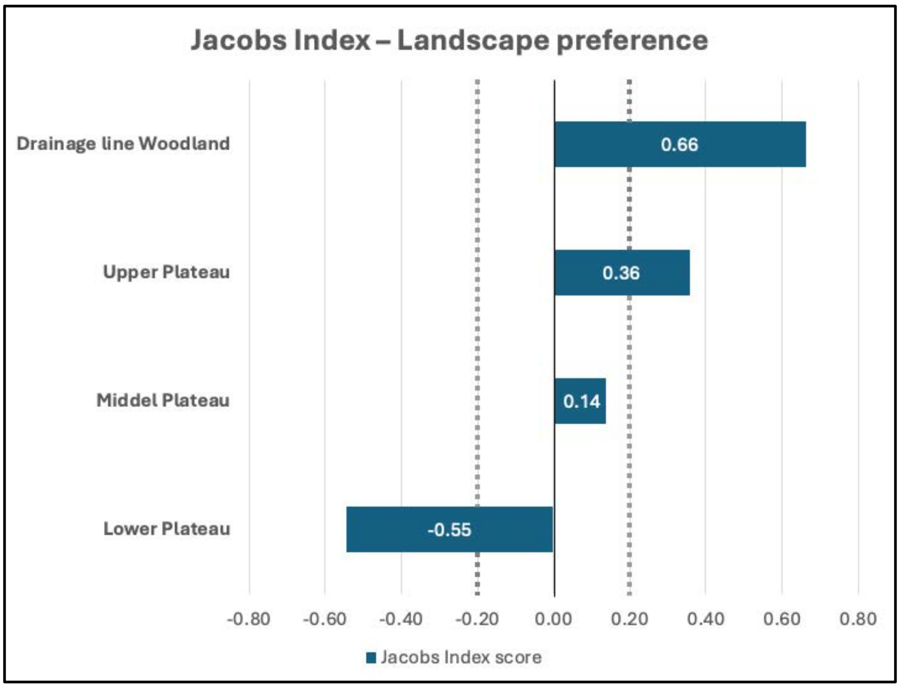

Figure 4.3 Study site selectivity analyses (Jacob's Index) of lion hunting landscape preference based on 144 kills sites located between March 2021 and May 2022. This selectivity index ranges from −1 indicating strong disfavour to 1 indicating a strong selective preference. Index scores of between 0.2 and -0.2, indicated as dashed grey line, show no particular preference.

4.3.3 Terrain and vegetation characteristics

Thirteen of the 16 measured terrain and vegetation parameters showed significant differences between the characteristics of kill sites vs. control sites, they are; the minimum visibility and average visibility at a height of 0.4 m and 1.5 m, % tree cover within a 5 m and 15 m radius, tree density score within a 5 m and 15 m radius, the grass/shrub height score within a 5 m and 15 m radius, % rockiness at a 5 m radius, and the rockiness score within a 5 m radius. The characteristics that displayed no significance were % grass/shrub cover within a 5 m and 15 m radius, rockiness score within a 15 m radius and % rockiness at a 15 m radius.

Visibility

Overall visibility, was significantly different between kill and control sites (Fig. 4.4). The average visibility score at a 1.5 m height was significantly lower (t = 4.58 df = 211, $P < 0.001$) at kill sites ($\overline{x}$ = 29.74 ± *SE* 2.82) than at control sites ($\overline{x}$ = 53.96 ± *SE* 4.46). The minimum visibility distance at a 1.5 m height was significantly lower (t = 5.783 df = 211, $P < 0.001$) at kill sites ($\overline{x}$ = 8.176 ± *SE* 1.12) than at control sites ($\overline{x}$ = 20.82 ± *SE* 1.87). The average visibility distance at a 0.4 m height was significantly lower (t = 3.34 df = 211, P < 0.001) at kill sites ($\overline{x}$ = 4.55 ± SE 0.356) than at control sites ($\overline{x}$ = 7.58 ± SE 0.830). The minimum visibility score at a 0.4 m height was significantly lower (t = 2.631 df = 211, P < 0.01) at kill sites ($\overline{x}$ = 1.31 ± SE 0.081) than at control sites ($\overline{x}$ = 2.1 ± SE 0.358).

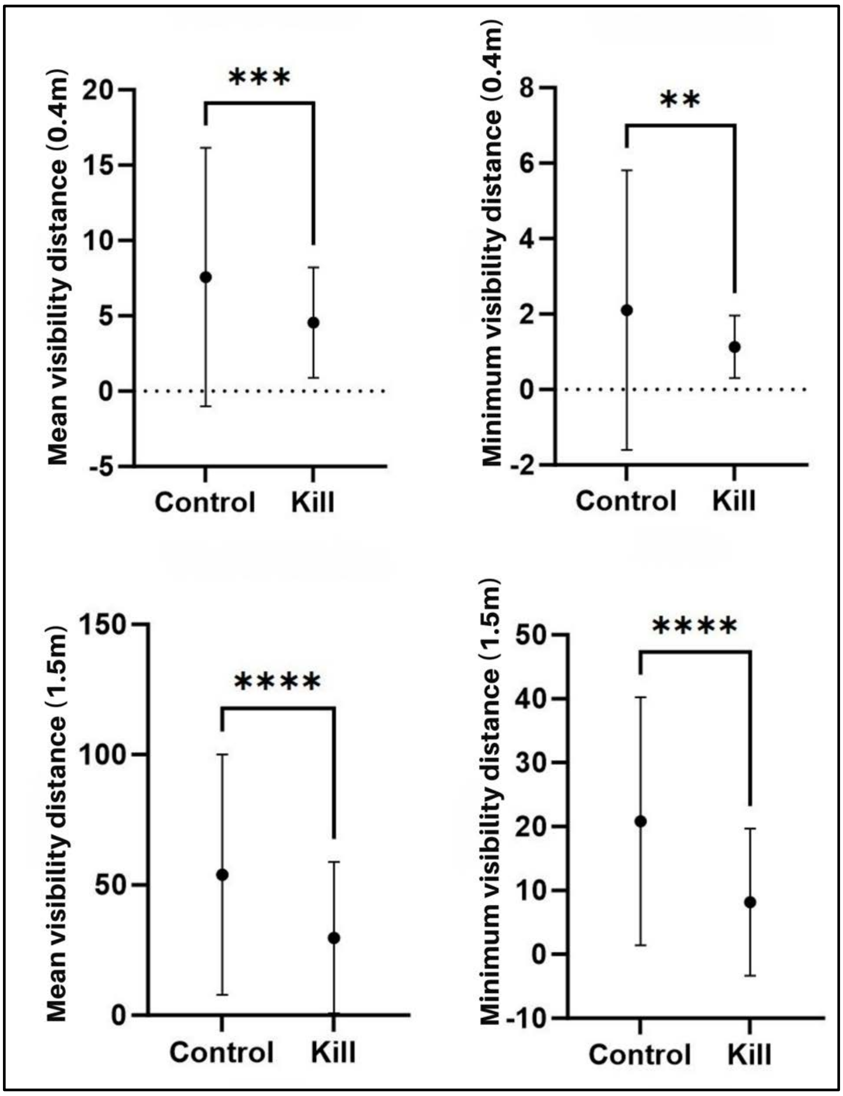

Figure 4.4 The visibility characteristics compared, using the t-test, between the control sites and the kill sites. The significance or non-significance is displayed as follows: ns = no significance and P ≥ 0.05, * = P < 0. 05, * *= P < 0. 01, *** = P < 0. 001, **** = P < 0. 0001. The error bars show standard deviation (SD).

Grass and shrub cover and height

The grass/shrub height score within a 5 m radius was significantly higher (t = 4.422 df = 211, P < 0.0001) at kill sites ($\overline{x}$ = 3.726 ± SE 0.14) than at control sites ($\overline{x}$ = 2.981 ± SE 0.095) while the percentage grass/shrub cover within the same radius was not significantly different (t = 0.743 df = 211, P = 0.458) between kill sites ($\overline{x}$ = 41.82 ± SE 2.51) and control sites ($\overline{x}$ = 39.39 ± SE 2.1). The grass/shrub height score within a 15 m radius was significantly (t = 3.257 df = 211, P = P < 0.01) higher between kill sites ($\overline{x}$ = 3.78 ± SE 0.11) than control sites ($\overline{x}$ = 3.32 ± SE 0.092) while the. percentage grass/shrub cover within the same radius was not significantly different (*t* = 1.057 *df* = 211, *P* = 0.292) between kill sites ($\overline{x}$ = 44.60 ± *SE* 2.22) and control sites ($\overline{x}$ = 41.45 ± *SE* 2.0) (Fig. 4.5).

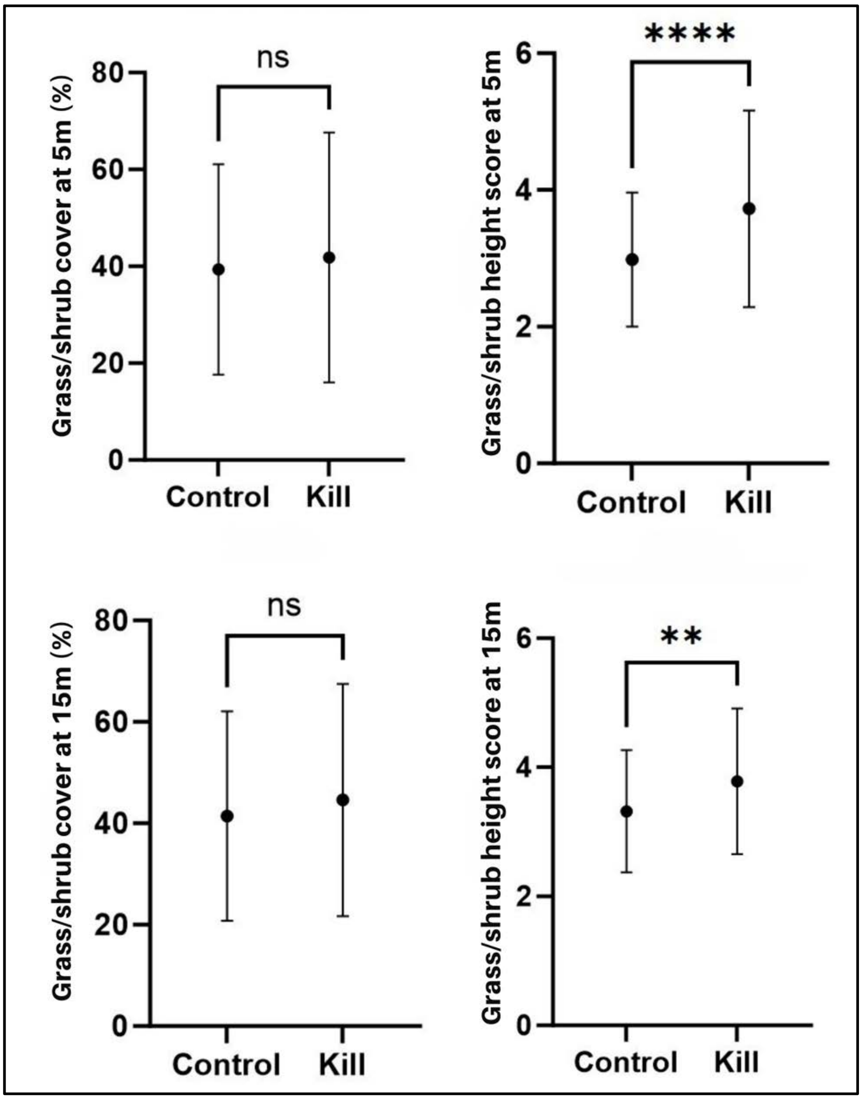

Figure 4.5 A t-test comparison between kill and control site grass/shrub cover and height characteristics. Cover were estimated as a % within a 5 and 15 m radius around the centre of a kill or control site, while the general height of grass and shrubs were estimated and then reported in accordance to 7 point score (see Table 4.3 for a descriptions of each score). The significance or non-significance is displayed as follows: ns = no significance and *P* ≥ 0.05, * = *P* < 0. 05, * *= *P* < 0. 01, *** = *P* < 0. 001, **** = *P* < 0. 0001. The error bars show standard deviation (SD).

Tree cover and density

Tree coverage and density were significantly different between kill and control sites, with all four recordings proving significant (Fig. 4.6). The tree density score within a 5 m radius was significantly higher (*t* = 5.972 *df* = 211, *P* < 0.0001) at kill sites ($\overline{x}$ = 2.33 ± *SE* 0.133) than at control sites ($\overline{x}$ = 1.393 ± *SE* 0.085). The percentage tree cover within a 5 m radius was also significantly higher (*t* = 5.446 *df* =

211, $P < 0.0001$) between kill sites ($\overline{x}$ = 16.56 ± SE 2.24) and control sites ($\overline{x}$ = 3.505 ± SE 0.881). The tree density score within a 15 m radius was significantly higher (t = 6.003 df = 211, $P = P < 0.0001$) between kill sites ($\overline{x}$ = 2.425 ± SE 0.112) than control sites ($\overline{x}$ = 1.589 ± SE 0.083). The percentage tree cover within a 15 m radius was also significantly higher (t = 5.705 df = 211, $P < 0.0001$) between kill sites ($\overline{x}$ = 17.94 ± SE 2.00) and control sites ($\overline{x}$ = 5.374 ± SE 0.942).

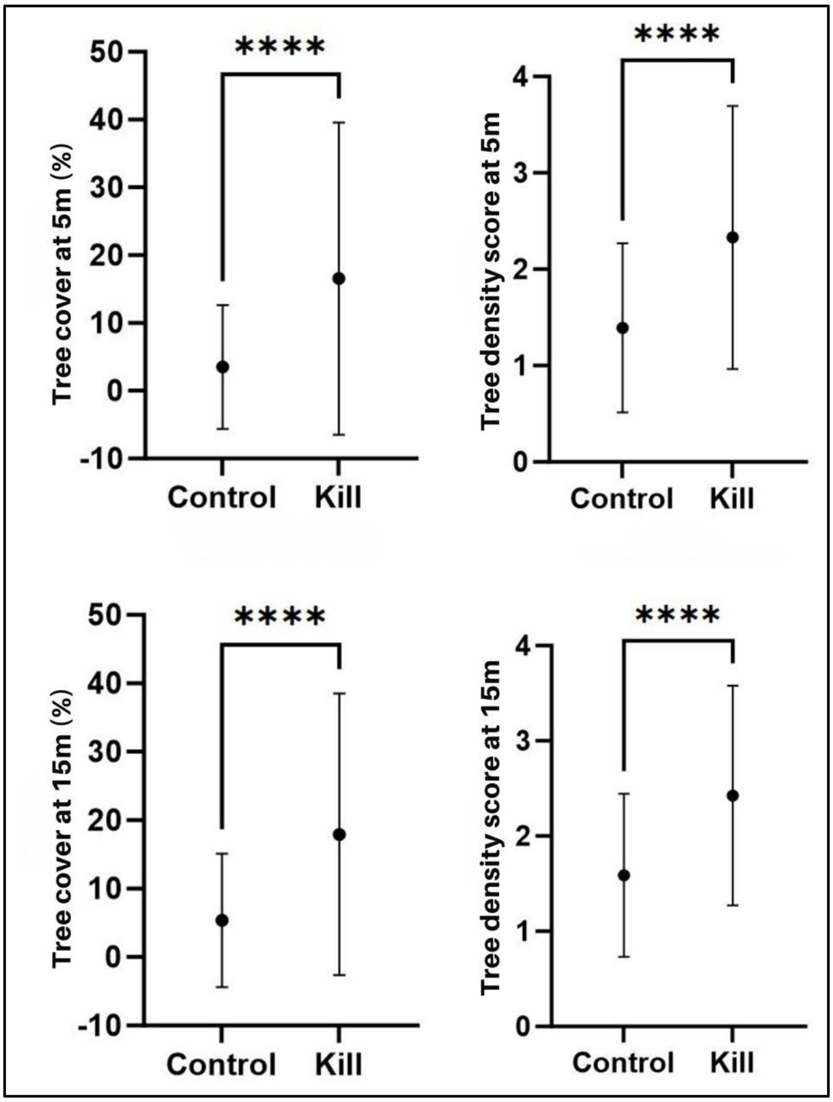

Figure 4.6 The tree cover and density characteristics compared, using the t-test, between the control sites and the kill sites. Tree cover was estimated as a percentage within a 5 m and 15 m radius of a kill and control site centre, while the density of trees was estimated and reported on using five point score (see Table 4.4 for a description of each score). The significance or non-significance is displayed as follows: ns = no significance and $P \geq 0.05$, * = $P < 0.05$, * *= $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$. The error bars show standard deviation (SD).

Terrain Rockiness

Rock cover estimates as a percentage and categorical score were significantly different within a 5 m radius, but was not significant within a 15 m radius from the kill site or control site centre (Fig. 4.7). The terrain rockiness score within a 5 m radius was significantly lower (t = 2.545 df = 211, $P < 0.05$) at kill sites ($\overline{x}$ = 2.472 ± *SE* 0.103) than at control sites ($\overline{x}$ = 2.860 ± *SE* 0.112). The percentage rocky coverage within a 5 m radius was also significantly less (t = 2.603 df = 211, $P < 0.01$) at kill sites ($\overline{x}$ = 30.57 ± *SE* 2.65) than at control sites ($\overline{x}$ = 40.79 ± *SE* 2.89). The terrain rockiness score within a 15 m radius was not significantly different (t = 1.699 df = 211, P = 0.091) between kill sites ($\overline{x}$ = 35.04 ± *SE* 2.67) and control sites ($\overline{x}$ = 41.7 ± *SE* 2.87). The percentage rocky coverage within a 15 m radius was also not significantly (t = 1.899 df = 211, P = 0.059) different between kill sites ($\overline{x}$ = 2.632 ± *SE* 0.101) and control sites ($\overline{x}$ = 2.916 ± *SE* 0.11).

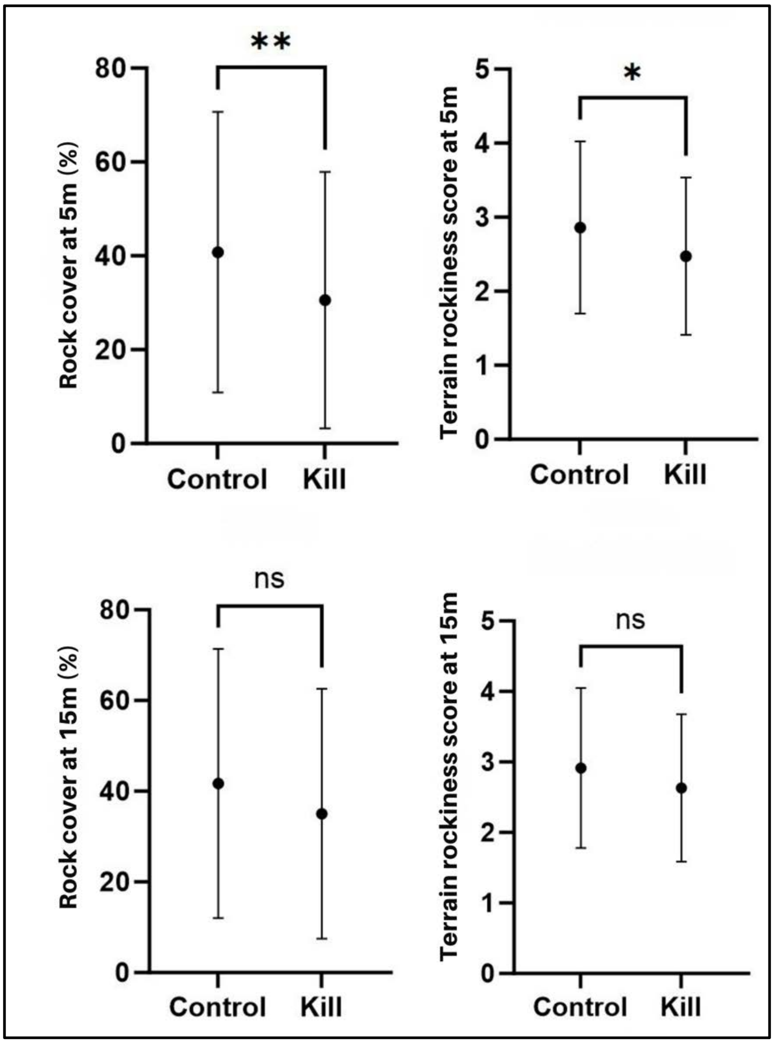

Figure 4.7 The terrain rockiness characteristics compared, using the t-test, between the control sites and the kill sites. Rock cover was estimated as both a percentage and categorical score within a 5 m and 15 m radius (see Table 4.5 for a breakdown of the different cover class scores). The significance or non-significance is displayed as follows: ns = no significance and $P \geq 0.05$, * = $P <$ 0. 05, * *= $P <$ 0. 01, *** = $P <$ 0. 001, **** = $P <$ 0. 0001. The error bars show standard deviation (SD).

4.3.3 *Prey availability/dung counts*

The dung counts, as a fine scale proxy for prey availability showed no significant difference in count numbers (t = 1.167 df = 211, P = 0.245) between kill sites (= 2.472 ± SE 0.103) and control sites (= 2.860 ± SE 0.112) (Fig. 4.8).

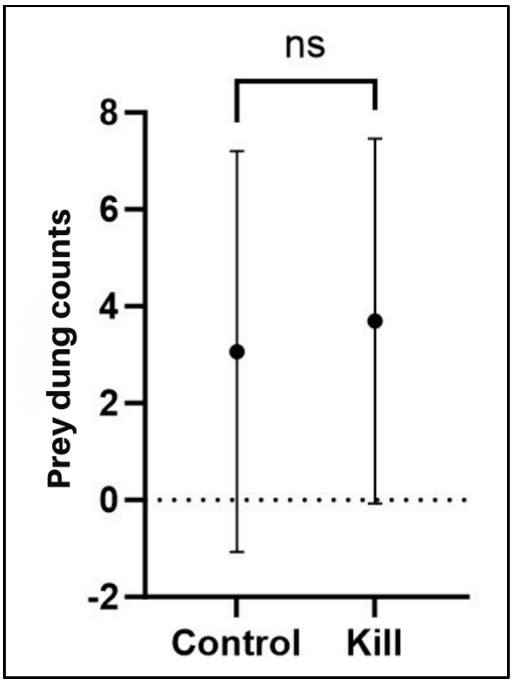

Figure 4.8 A t-test comparison of dung count numbers around lion kill and control sites. The number of herbivore dung pellet groups were counted along four 60 m transects radiating from the centre of kill and control sites (see text for more detail). The significance or non-significance is displayed as follows: ns = no significance and $P \geq 0.05$, * = P < 0. 05, * *= P < 0. 01, *** = P < 0. 001, **** = P < 0. 0001. The error bars show standard deviation (SD).

4.4 Discussion

In this study, most of the fine scale kill site visibility, vegetation and terrain characteristics are significantly different from those of the measured control sites. In contrast, fine scale prey availability, as measured using dung counts, were not significant between kill and control sites. These contrasting results suggest that prey catchability rather than prey availability dictate lion kill site locations. There is also a clear difference in preference for the different landscapes as hunting areas and the different landscapes must now be investigated at a broad scale to see if these landscapes differ significantly with regards to overall visibility, vegetation and terrain characteristics.

There were proportionally more kill sites in drainage lines, middle- and upper-level landscapes while the flat lowland bottomlands with sparse vegetation had far less kill sites than expected given the size of the respective areas. Carnivores select habitats that increase probability of hunting success and hence, select habitat features that increase susceptibility of prey to predation (Hopcraft *et al.*, 2005; Balme *et al.*, 2007; de Boer *et al.*, 2010). I recorded a high preference for drainage line woodland, which comprises of the most densely covered vegetation in the reserve (Bezuidenhout, 2016; Spies, 2017a) and could potentially be attributed to the cover available (Hopcraft *et al.,* 2005; Davidson *et al.*, 2012; Loarie *et al.*, 2013; Davies *et al.*, 2016). Additionally, the preference for drainage line woodland may link to areas where lions spend the majority of their time moving and resting and, thus, the probability of catching near to denser shaded areas is more likely (Young *et al.*, 2013).

In arid and semiarid regions, such as KrNP, herbivores tend to aggregate around scarce water sources (Thrash *et al.,* 1995; Davidson *et al.*, 2012), and for most herbivores, habitat selection is largely influenced by distance to water (Valeix *et al.,* 2009; de Boer *et al.*, 2010; Tarugara *et al.*, 2024). In KrNP, the drainage lines generally have more moisture and retain water in pools for longer (Spies, 2017a) than in the more open terrain and is available for lions to drink (Mosser *et al.*, 2009; Valeix *et al.,* 2009; Davidson *et al.*, 2012; Tarugara *et al.*, 2024). Although water-dependency, or independency, should influence the movements (Redfern *et al.,* 2003), of the six large prey species for lions in KrNP, only red hartebeest and zebra are reliant (or partially) upon regular water (Skinner & Chimimba, 2013; Owen-Smith, 1996). In addition to responding to prey, large cats are also known to use drainage lines to traverse a landscape (de Boer *et al.*, 2010) and thus may encounter prey in a similar landscape. While traversing the study area extensively for this research it became apparent that there a numerous uncharted pools in streams, as well as springs that in addition to the artificial waterpoints provide water to both prey and predators. Assessing kill site locations in relation to artificial waterpoint positions to ascertain whether it plays a role in kill site distributions was thus not considered as it is certainly not the sole source of water for a greater part of the year. During times of drought the situation might be different.

The upper plateau was also preferred. Here higher rainfall results in a more montane grassland landscape (Bezuidenhout, 2016; Spies, 2017a; Sargent *et al.*, 2021), with a greater grass coverage and high productivity that, according to studies in savanna environments, could encourage a higher abundance of prey (Spong, 2002; Balme *et al.*, 2007; Maruping-Mzileni *et al.,* 2017; Sargent *et al.*, 2021). Conversely, the avoidance of the Lower Plateau may be attributed to the absence of cover for, both, good places to rest and/or good cover to conduct a successful hunt. I suggest a detailed future investigation on prey spacial and temporal distribution within the KrNP that can help us to understand lion landscape preference for killing.

Lions are opportunist stalk-and-ambush hunters that require a combination of good cover to get close to their prey and then acceleration, large body weight and, occasionally, good social coordination in order to conduct a successful hunt (Schaller, 1972; Radloff & Du Toit, 2004; Hopcraft *et al.*, 2005). The cover is required to conceal a lion whilst either ambushing or stalking its prey (Hopcraft *et al.*, 2005; Kittle *et al.*, 2016). Too much cover, however, can either impede the progress of a stalk by obstructing a clear view of the target and pathway to the target which can increase the chance of detection by prey due to a noisier approach (Balme *et al.*, 2007). Additionally, it is possible that cover may not be for the sole purpose of hunting. For instance, landscapes with high cover provide more resting sites in the shade of trees (Hayward *et al.,* 2007; Loarie *et al.*, 2013; Davies *et al.*, 2016), which is also likely linked to conditions that prey may choose especially in the hot dry season (Georgiadis *et al.,* 2003; Martin *et al.*, 2015).

There are multiple physical features that could contribute to preferred hunting habitat such as, tree density, grass and shrub cover, fine scale landscape curvature, distance from water, slope and terrain rockiness (Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Valeix *et al.*, 2010; Davidson *et al.*, 2012; Riginos, 2015; Wheatley *et al.*, 2021). This study found visibility at a 1.5 m height around kill locations to be significantly more restricted than at control sites. The 1.5 m height considerd to emulate the vision that a large herbivore would generally have (Davies *et al.*, 2021), suggests that a large herbivore would have significantly reduced chances to see lion stalking, or ambushing, in the areas where they succumbed. Furthermore, the visibility at 0.4 m height, deemed sufficient for a lion to conceal themselves (Elliot *et al.*, 1977) is also significant where there is greater cover at the kill site than at the non-kill sites. The height of the grass/shrub cover around the kill sites, at both 5 m and 15 m radii, were also significantly higher than at control sites, but the percentage cover was not significant. This suggest that the height of the cover may be more important than the density of the cover. Furthermore, both tree cover and density, at 5 m and 15 m radii, were also significantly higher at kill sites further supporting the notion that cover and associated reduction in visibility aid lions in making successful kills (de Boer *et al.*, 2010; Davies *et al.*, 2016). Additionally, it is likely that kill sites also associate with the presence of good resting sites (Young *et al.*, 2013).

The rockiness of the terrain at 15 m measurements displayed no significant difference between kill and control sites whereas the immediate vicinity around the kill site centre (5 m radius), identified from stomach content remains, were less slightly less rocky than at control sites. Considering that the difference is only apparent very close to the considered centre of the kill site, it is possible that the carcasses were dragged to slightly flatter, more comfortable terrain to feed upon (Loarie *et al.*, 2013).

Multiple studies suggest that herbivore abundance is an influential factor determining the abundance of large carnivores on a broad scale (East 1984; Ritchie & Olff 1999; Hopcraft *et al.*, 2005). In this study there was a lack of fine scale differences in prey abundance suggesting that the lions at the fine scale level sought out areas where prey were easier to catch. The difference in landscape scale kill site preference might be driven by broad scale prey distribution patters. These broadscale prey distribution patterns were not assessed in this study as the available prey location data, as obtained from the annual aerial census, could not reliably place animals in either the narrow drainage line habitat or surrounding landscape.

Predator behaviour and the potential preference of areas where prey are more catchable, irrespective of prey abundance, is not as comprehensively understood (Hopcraft *et al.*, 2005) but appears to be important in KrNP. Not only are there fine scale differences in visibility and vegetation cover between kill and non-kill sites, but are there clear preference for certain landscapes for killing large prey. For example, the upper plateau and drainage line woodland represent only 9% of the entire reserve but are considered the preferred broad hunting landscapes for lions. This suggests that lions only efficiently use a small portion of the entire KrNP, a factor that could significantly impact lion management and their numbers. Future studies should examine the distribution of visibility and vegetation cover across KrNP, as these features likely define suitable hunting habitat for lion in this reserve. A limitation in the extent of such habitats might restrict lion populations, irrespective of prey abundance, as lions clearly do not make kills randomly across this landscape.

4.5 Conclusion

Landscape attributes have been shown to be significant factors driving resource selection in carnivores (Van Orsdol, 1984; Stephens & Krebs, 1986; Spong 2002; Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Riginos & Grace, 2008; Davidson *et al.*, 2012; Tambling *et al.*, 2012; Loarie *et al.*, 2013; Davies *et al.*, 2016; Smith *et al.* 2020). The aim of this investigation was to understand whether there are preferred feeding sites for lions within the KrNP and, what are the key ecological determinants of these preferred feeding sites. The expectation that lions would feed in areas that have dense vegetation and cover, held true in my study. This result indicates that not all of the KrNP necessarily provides suitable hunting habitat for lions in this semi-arid environment.

This preference to hunt in areas with dense vegetation and cover suggests that the lions only prefer a small portion and not the entire 883 km^2 of the KrNP, as vegetation cover is extremely heterogenous and sparse within KrNP. Thus, the fight for territories and the use of the areas with dense vegetation can increase pressure between lions when competing for resources. This fight for limited resources would be an important aspect to consider if the park were to increase in size. When considerations for park expansion are made drainage line woodland and upper plateau landscapes should be prioritised as an increase in coverage of these habitats should be beneficial for the lion population.

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CHAPTER 5

RESEARCH FINDINGS AND MANAGEMENT IMPLICATIONS

Knowledge of lion (*Panthera leo*) dietary intake is essential for understanding of their behaviour and influence on prey populations (Barnardo *et al.,* 2020; Beukes *et al.,* 2020). Lions are known to display a diverse diet (Hayward & Kerley, 2005; Hayward & Kerley, 2008) and are generally not specialist feeders (Fryxell *et al.*, 2022), but have been recorded to specialise in certain areas such as the Skeleton Coast National Park in the northwest of Namibia (Stander, 2019). In the Karoo National Park (KrNP) the lions preyed on 10 different species, of which six were over 50 kg in weight. The six large species were - common eland (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiceros*), red hartebeest (*Alcelaphus buselaphus caama*), gemsbok (*Oryx gazella*) zebra (mostly Cape mountain zebra *Equus zebra zebra*, with a few Burchells zebra *Equus quagga*) and Ostrich (*Struthio camelus*) – and contributed 98% towards the prey biomass consumed by lion within the KrNP. The recent large prey diet, within the KrNP, comprised predominantly of four species - common eland, greater kudu, red hartebeest and gemsbok – that contributed 89% to the total diet and 91% to the total biomass consumed. These findings are corroborated by the historic diet analysis where it was found that from 2011 to 2022, 87% of the total diet is made up of these same four species - eland (19%), kudu (27%), red hartebeest (19%) and gemsbok (22%). It will be beneficial to get a better understanding of the small species contribution to the diet as well. Within KrNP there are a number of smaller prey species such as springbuck (*Antidorcas marsupialis*) and porcupine (*Hystrix africaeaustralis*) that have been shown to play an important part "top ups" between large prey kills (Eloff, 1984; Hayward & Kerley, 2005). It has also been reported that the springbok population is struggling to recover after an extensive translocation programme reduced springbuck numbers markedly in 2010 (Ferreira & Gaylard, unpublished) which coincided with the period of lion introduction. Establishing the extent of springbuck use in KrNP lion diet can thus assist management acertain the cause of the slow recovery in springbuck numbers. The small species contribution to the diet is currently under investigation using scat analysis.

Even though the lion diet was dominated by the same four species throughout the period since reintroduction (2010), lion displayed the ability to vary the contribution of these key species over the 12-year period. The yearly contribution of eland varied from 9% - 28%, red hartebeest from 9% - 27%, kudu from 14% - 41%, gemsbok from 14% - 34%. Even some of the less consumed large prey seems to vary in their importance by as much as 20% such as zebra 5% – 25%. Lion diet is known to change in response to shifting ecological conditions over time (Schaller, 1972; Stander, 1992b; Owen-Smith &

Mills, 2008; Davidson *et al.*, 2013; Fourie *et al.*, 2015). Prey switching can aid in the persistence of predator–prey systems in small fenced reserves where natural immigration of prey is not possible (Bisset *et al*., 2012). In 2019, at the peak of the drought in KrNP (Moeletsi *et al.,* 2022), lions preferred gemsbok and zebra significantly more than in the other years, while still preferring, but less so, eland and kudu. This prey switch was short in duration and is believed to be linked to the environmental conditions at the time, similar to other cases like in the Kruger National Park (Mills *et al.*, 1995; Maruping-Mzileni *et al.,* 2017) and Eastern Cape (Bisset *et al*., 2012).

The overall abundance of the four key prey species - eland, kudu, gemsbok and red hartebeest - thus seems to be important for lion subsistence rather than particularly high numbers of any particular one of the four species. Monitoring and managing the balance between the lion population numbers and the availability of these four prey species are thus essential to limit potential breakouts in search of food. Lions displayed a prey switch, at the peak of the drought in 2019, when eland numbers were 589 and kudu numbers were 443. These numbers further decreased to 516 and 414 respectively in 2021. I would recommend, given that lion numbers exceeded the current number of 11 individuals in 2019, that the park management should aim to keep the eland population above 600 individuals and the kudu above 450 individuals if expansion of the lion population is considered. Additionally, in 2019, 970 gemsboks and 830 zebras were counted which, resultantly, became the selected species that year. I'd recommend these two species remain collectively above 1600 individuals. These numbers should be considered when decisions on herbivore population size management are made.

Furthermore, aside from availability of prey, the catchability of prey, and in essence the availability of optimal hunting habitat, in KrNP is an important factor to consider from a lion management point of view. Multiple studies found that vegetative cover is a significantly preferred attribute at kill sites (Hopcraft *et al.,* 2005; Loarie *et al.*, 2013; Davies *et al.*, 2016), which provides sufficient concealment for the lions to stalk and successfully kill (Van Orsdol, 1984; Elliot, 1977; Hopcraft *et al.,* 2005). The lions in the KrNP displayed a similar preference. However, dense vegetative cover is limited within KrNP and the landscape is extremely heterogenous (Bezuidenhout, 2016). The opportunity for lions to kill prey, even if available, might thus be constrained by the lack of stalking cover. At a broader landscape level, the largest landscape type, the lower plateau (covering 71% of the entire KrNP), had much less lion kills than expected for its size. In contrast the smallest landscape type of drainage line woodland (covering only 4%), was the most preferred kill site location. This is an additional indication that vegetative cover is a significant influence as the lower plateau has the least overall vegetative cover and the drainage line woodland the most. The middle plateau (covering 5%) and the upper plateau (covering 20%) having pockets of dense vegetation (Bezuidenhout, 2016). Seeing that the majority of the KrNP landscape in the study area, and thus arguably the rest of the park, was not identified as preferred hunting habitat by lion the limited optimal hunting habitat must be considered important for lion persistence.

Given the scarcity of optimal hunting habitat the lions in KrNP should be competing for territories with the highest portion of these preferred areas and its associated prey (Loveridge *et al.*, 2009; Valeix *et al.*, 2012; Tuqa *et al.*, 2014; Mosser *et al.*, 2015). These areas of best lion habitat have not been demarcated within KrNP, although evidence suggest it are the drainage woodland and upper plateau landscapes, but the opportunity exists by analysing the lion location data of the past 12 years as provided by the 22 lions that have been collared during this period. The fight for territories in key areas might play a role in breakouts of lions, as the dominant prides may potentially use most of the limited optimal hunting habitat forcing other prides, un-associated individuals, or younger males, to find and hunt prey in generally avoided suboptimal hunting habitat. Thus, the limitation in optimal hunting habitat needs to be identified and careful considered when thinking about lion number management within KrNP. Identifying the key lion habitats will help to better understand the pride dynamics and territories in relation to the different landscape types. Collectively the drainage line woodland and upper plateau, within which proportionally the most kill sites were found per unit area, only make up 9% of the entire reserve. It is thus recommended that these two landscapes are carefully managed to avoid habitat degradation and considered a priority in reserve expansion plans. With the inclusion of more optimal hunting habitat the lion population can potentially be increased, which can then allow KrNP to make a greater contribution to the lion meta population of South Africa (Selier et al., 2024).

Effective management of free-roaming large predators requires an understanding of what predator densities are sustainable (Clements *et al.,* 2016). Even though some studies have been conducted on the predator carrying capacity of regions, Hayward *et al.* (2007) states that conservation managers had no way of knowing the carrying capacity of the areas they manage. Carrying capacities have multiple factors that influence their relationships including the difficulty of censusing carnivores, variations in methodology, appropriate definitions of food density, interspecific competition and intra-guild predation, genetics and disease (Fuller & Sievert, 2001). However, carnivore densities generally reflect the abundance of their prey and available biomass (Bertram, 1975; Fuller and Sievert, 2001; Clements *et al.*, 2016).

Hayward *et al.* (2007) further suggests that calculating predator carrying capacity - using their equation that takes available prey populations into account - annually after wildlife censuses could determine whether management actions are required to increase prey populations or decrease the predator populations present (Brook *et al.,* 1997). This can also lead to a better understanding of an areas ability to support a viable predator population, albeit limited (Hayward *et al.,* 2007). By analysing the preferred prey species populations, within the known preferred weight ranges (Hayward & Kerley, 2005) the resultant costs of large predator management may also be reduced (Hayward *et al.,* 2007). As the preferred lion prey species in the KrNP, the presence of kudu, eland, gemsbok and red hartebeest need to be carefully monitored and considered in lion carrying capacity calculations. I consider that if these four large prey species are effectively conserved and their numbers recover, following the drought, the number of lions within KrNP should be able to increase. However, it will be important to continue the monitoring of prey numbers and especially the mentioned four key species, while keeping close track of lion space use of optimal and sub-optimal habitat and any lion break-outs. Using this data, it is important to assess if there is any correlation between lion numbers, key habitat use, the numbers of preferred prey and breakouts.

The lowest lion densities predicted by Hayward *et al.* (2007) are for new populations in newly restocked areas where the founder prey population base is still growing or in arid areas that generally support low wildlife densities, such as arid and semi-arid regions like the KrNP. Even though Hayward *et al.* (2007) believes their estimates to be accurate and conservative across most of the habitats where Africa's large predators occur. Considering the potential dire consequences of overpopulation of large predators (Hunter, 1998; Power, 2002), traditional carrying capacity estimates, like that of Hayward *et al.* (2007) are to be treated with caution for the KrNP due to the extreme heterogeneity of vegetative cover and optimal hunting habitat.

Ultimately, a combination of a reduction in overall prey numbers, especially the four key prey species, and competition for key hunting habitat to capture the prey should be considered when contemplating the breakouts of lion other that young males dispersing due to pressure from resident male coalitions. Additionally, lions are known to have large territories within arid areas (Beukes, 2016; Stander, 2019) and even though these territories may hold sufficient prey populations the preferred hunting habitat within the territory, as displayed in this study, may be limited and far apart. This scarcity may force lions to travel further to secure the necessary food to meet their energy requirements. Ultimately, prey catchability, more so than abundance, appears to be the restricting factor here and should be considered more in other places where lions persist within areas with similar vegetation and terrain cover.

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APPENDICES

Appendix A - The 57 mammal species historically recorded in Karoo National Park (adapted from SANParks, 2023)

Common Name	**Scientific Name**
Small Mammals	
Cape rock elephant-shrew	*Elephantulus edwardii*
Common Molerat	*Cryptomys hottentotus*
Forest shrew	*Myosorex varius*
Grant's rock mouse	*Aethomys granti*
Grey pygmy climbing mouse	*Dendromus melanotis*
Hairy-footed gerbil	*Gerbillurus paeba*
Karoo bush rat	*Otomys unisulcatus*
Lesser dwarf shrew	*Suncus varilla*
Lesser red musk shrew	*Crocidura hirta*
Multimammate mouse	*Mastomys natalensis*
Namaqua rock mouse	*Micaelamys namaquensis*
Pouched mouse	*Saccostomus campestris*
Pygmy mouse	*Mus minutoides*
Round-eared elephant-shrew	*Macroscelides proboscideus*
Saunders' vlei rat	*Otomys saundersiae*
Short-tailed gerbil	*Desmodillus auricularis*
Smith's rock elephant-shrew	*Elephantulus rupestris*
Spectacled Dormouse	*Graphiurus ocularis*
Striped mouse	*Rhabdomys pumilio*

Medium and large mammals

Carnivore

African Wildcat	*Felis lybica*
Bat-eared Fox	*Otocyon megalotis*
Brown Hyena	*Parahyaena brunnea*
Cape Clawless Otter	*Aonyx capensis*
Cape Fox	*Vulpes chama*
Caracal	*Caracal caracal*
Lion	*Panthera leo*

Omnivore

Chacma Baboon	*Papio ursinus*
Small Grey Mongoose	*Galerella pulverulenta*
Small-spotted Genet	*Genetta genetta*
Striped Polecat	*Ictonyx striatus*
Suricate	*Suricata suricatta*
Vervet monkey	*Chlorocebus pygerythrus*
Water Mongoose	*Atilax paludinosus*
Yellow Mongoose	*Cynictis penicillata*

Insectivore

Aardwolf	*Proteles cristata*
Antbear (Aardvark)	*Orycteropus afer*
Cape serotine bat	*Neoromicia capensis*
Common split-faced bat	*Cynictis penicillata*
Melck's serotine bat	*Neoromicia melckorum*

Herbivore

Black Rhinoceros	*Diceros bicornis*
Burchell's Zebra with Quagga bred characteristics	*Equus quagga burchellii*
Cape Mountain Zebra	*Equus zebra zebra*

Common Duiker	*Sylvicapra grimmia*
Eland	*Taurotragus oryx*
Gemsbok	*Oryx gazella*
Grey Rhebuck	*Pelea capreolus*
Klipspringer	*Oreotragus oreotragus*
Kudu	*Tragelaphus strepsiceros*
Mountain reedbuck	*Redunca fulvorufula*
Red Hartebeest	*Alcelaphus buselaphus caama*
Rock Hyrax	*Procavia capensis*
Springbok	*Antidorcas marsupialis*
Steenbok	*Raphicerus campestris*
Cape Hare	*Lepus capensis*
Scrub Hare	*Lepus saxatilis*
Riverine Rabbit	*Bunolagus monticularis*
Smith’s Red Rock Rabbit	*Pronolagus rupestris*
Porcupine	*Hystrix africaeaustralis*

Appendix B - The historic kill data from 2010 – 2020, with 2021 and 2022 being from the field work of this study. RHB = Red Hartebeest.

Species	**2010 2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**
Eland	11	8	13	33	21	24	22	12	18	7	25	6
Gemsbok	17	8	28	24	17	33	22	13	30	11	11	6
Kudu	8	8	61	31	16	44	26	20	14	14	19	9
Ostrich	2	2	5	4	3	1	0	0	1	0	4	0
Zebra	15	3	8	7	6	20	8	5	18	3	4	5
RHB	6	8	32	17	14	46	21	11	8	8	18	12
	59	**37**	**147**	**116**	**77**	**168**	**99**	**61**	**89**	**43**	**81**	**38**

Appendix C - The total number and percentage contributions of large prey species to lion diet derived from GPS cluster analysis in KrNP between March 2021 and May 2022, and the average weight of the respective large prey species (used for biomass calculations) taken from Skinner and Chimimba (2005). RHB = Red Hartebeest.

Large Prey Species	**No. of kills recorded**	**Percentage Contribution (%)**	**Average weight (kg) ***
Eland	31	26.05	296
Kudu	28	23.53	152
Ostrich	4	3.36	69
Gemsbok	17	14.29	210
Zebra	9	7.56	234
RHB	30	25.21	120
Total	**119**	**100**	

* Average weights taken from Skinner & Chimimba (2005)

Appendix D - The total large prey counts from the annual aerial census counts (from 2010 – 2021) within the KrNP.

	2010	**2011***	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020****	**2021**
Eland	333	*471*	609	583	637	744	755	857	1116	589	*553*	516
Gemsbok	1447	*1783*	2119	2582	2457	1555	1659	1948	1387	970	*907*	843
Kudu	678	*781*	884	512	888	909	662	897	609	443	*429*	414
Ostrich	579	*789.5*	1000	1109	645	607	437	439	403	418	*366*	313
Zebra	686	*788.5*	891	929	932	1088	1005	970	921	830	*818*	805
Red hartebeest	1237	*1550*	1863	2105	2008	1650	1630	1429	1183	906	*873*	840
Total	**4960**	**6163**	**7366**	**7820**	**7567**	**6553**	**6148**	**6540**	**5619**	**4156**	**3944**	**3731**

* 2011 errorous count replaced by avg between 2010 and 2011

**2020 no count so values from avg between 2019 and 2021